A STUDY OF THE INTERACTIONS BETWEEN C_3 AND C_4 GRASSES ON SIGNAL HILL, CAPE TOWN.

MAANDA SOLOMON LIGAVHA

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TO MY DEAR MOTHER

(MAKWARELA MUDZHEGWA LIGAVHA)

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ABSTRACT

Current concerns with reference to global climate change can help us to focus on the competitive interaction of grasses with different photosynthetic pathways.

The dominance of eight different common grass species occurring on Signal Hill was investigated, and three species which occurred in localized dense stands were suitable for detailed investigation.

Distribution patterns of the three selected grass species, Hyparrhenia hirta (L.) Stapf (C_4), Merxmuellera disticha (Nees) Conert (C_3) and Themeda triandra Forsskal (C_4) were interpreted using a dispersion index (R). Regularity in dispersion of individual grasses was quite common, whilst aggregated and random dispersion was not.

Potential competitive interactions between those grasses (perennial) on the east- and west-facing slopes of Signal Hill were then described.

Using nearest-neighbour analysis it was possible to show that both inter- and intra-specific competition was occurring between the grass species investigated. Pattern analysis was supported by removal experiments and it was possible to infer that the three grass species are competing for water and space.

The measurements of carbon dioxide fixation rates under greenhouse conditions demonstrated that C_4 grasses were more competitive, relative to C_3 grass and responded more strongly to changes in soil moisture status. Species with the C_4 pathway showed substantial increase in photosynthetic rate in response to an increase in soil moisture content whilst a C_3 grass' carbon dioxide assimilation rate at those moisture content was relatively lower.

Seedling transplant experiments showed that monospecificity of patches could chiefly be attributed to familial clumping, limited seed dispersal, and vegetative reproduction.

Phenological aspects like growth, production, and reproduction in terms of flowering tillers of neighboured and non-neighboured individuals, and of individuals one year and

two years after fire, were studied to assess the importance of competitive interactions and fire.

The results of this study posed the following question: In the light of the global warming effect, which grass species (representing C_3 and C_4 pathways) are likely to prevail in different parts of the world?

CHAPTER 1

1.0: GENERAL INTRODUCTION

Studies of the distribution of grasses in South Africa have shown that C_3 and C_4 grass species are separated geographically (Vogel et al. 1978). Grass species having the C_4 pathway are more abundant than C_3 grass species over most of the country. The only areas where C_3 grass species predominate are the winter rainfall region of the Western Cape and the summits of the Drakensberg and other mountain ranges in the Eastern Cape, whilst C_4 grass species are abundant in the remaining summer rainfall regions (Vogel et al. 1978).

A number of studies have investigated the factors responsible for the distribution of C_3 and C_4 grasses along selected environmental gradients (Chazdon 1978; Tieszen et al. 1979; Boutton et al. 1980; Rundel 1980) and within broad geographical regions (Teerie and Stowe 1976; Ellis et al. 1980). Certain of these studies report that both temperature and rainfall are equally reliable as predictors of the relative occurrence of C_3 and C_4 grass species (Chazdon 1978; Tieszen et al. 1979; Boutton et al. 1980). A study of the distribution of C_4 grasses in South Africa (Vogel et al. 1978) indicates that the temperature during the growing season is the major factor accounting for the distribution and abundance of C_3 and C_4 species. Cowling (1983) found that C_3 grass cover is significantly correlated with increased post-disturbance vegetation age, low intensity grazing, high litter cover and cool, steep, poleward slopes.

After a pilot investigation I observed that some essentially tropical and subtropical C_4 grass species, such as H. hirta and T. triandra, prevail locally on both the east- and west-facing slopes of Signal Hill, Cape Town. Such a distribution pattern is anomalous to general expectations (i.e. C_3 grasses should dominate throughout the winter rainfall region of the Western Cape) and hence intriguing. I therefore undertook this study to

investigate what factors account for the observed distribution pattern. Motivating this study is also the common experience that C_4 grasses such as H. hirta and T. triandra are very important socio-economically (reported in sections 3.3.1a & c). Hypothetically, some form of disturbances (e.g. fire, grazing, vegetation removal) and competition were put forward as major factors responsible for the observed grass distribution patterns. For more on disturbance on Signal Hill, see Chapter 3, sections 3.0 to 3.2.

I addressed the following questions:

i) Are C_3 plants superior competitors under these condition?
ii) Is competition responsible for the observed grass distribution patterns on Signal Hill, or does anthropogenic disturbance (e.g. fire, vegetation removals and grazing) contribute to the observed grass distribution patterns?
iii) What effect does carbon uptake during the hot, dry summer season of the Western Cape have on C_3 and C_4 grass distribution patterns?

To attempt to answer all the questions referred to above, various scientific methods were utilized.

Spacing patterns of three perennial dominant grass species on the east- and west-facing slopes of Signal Hill were studied in detail. Specifically what was examined were the dispersion patterns (clumped, random and uniform) of individuals on both the slopes. The values of R (dispersion indices) were then calculated. From these values it was possible to judge whether there was any competitive interaction or not. Hill (1973) gives as one reason for the analysis of spacing pattern "suggesting or checking theories about competition and establishment of plants in the community". Several early workers found apparent regularity of plant spacing in deserts, and attributed this to competition (Shreve 1942; Went 1955, in Phillips and MacMahon 1981). Some ecologists vehemently disagree with this assumption, whilst others concur about the commonness and even

existence of regular patterns (Cottam 1955; Greig-Smith 1961; Turner 1962; Anderson 1967, 1970, 1971; Greig-Smith and Chadwink 1965; Anderson 1967; Beals 1968; Anderson; Malik and Jacobs 1969; Wright 1970; Waisel 1971; Wallace and Romney 1972; Barbour and Diaz 1973; King and Woodell 1973; Malik, Anderson and Myerscough 1976; Barbour et al. 1977b).

Nearest-neighbour analysis technique (Pielou 1960) was employed to investigate the two aspects of competition, that is, intensity and importance. Many ecologists failed to clarify the distinction between competition intensity and competition importance, and accordingly have strongly differed about the prevalence of competition as an agent of community structuring (Welden et al. 1988). For a more clear-cut differentiation between competition importance and competition intensity, these terms were clarified by Welden et al. (1988) as follows:

> competition is defined as the induction of physiological strain in an organism as a direct result of the use of resource items by another organism, whilst the importance of competition is the relative degree to which competition determines the physiological status or fitness of individuals, or growth rate of populations or the structure of the community, and the intensity of competition is the absolute severity of physiological strain induced. The intensity of competition and the importance of competition were respectively measured by the slope of any regression line (graph) and its coefficient of determination (r).

The study of photosynthesis was also of high-priority in this study because the competitive abilities of C_3 and C_4 plants could be compared experimentally and in the field. Existing data for fynbos growing in the mediterranean-type region of South Africa (fynbos), demonstrates that carbon dioxide assimilation rates decline with increasing water stress (Van der Heyden and Lewis 1989). There is also a common dogma among ecophysiologists that C_4 plants are generally

photosynthetically more competitive than C_3 plants. Under high light intensities, high temperature optima, and low intercellular CO_2 concentrations, C_4 plants are known to be photosynthetically advantaged (Black 1971; Bjorkman 1975). The quantum yield is greater for C_3 plants at low temperatures, and the C_4 pathway is disadvantaged under these conditions (Ehleringer and Bjorkman 1977).

I investigated competition mainly for water, because plant water availability may affect the rate of photosynthesis. Under optimal water supply the rates of photosynthesis for both C_3 and C_4 grass species are relatively high. Ecologists have inferentially adduced water, volume of space and other vital resources as being responsible for the survivorship of living organisms (Yeaton 1978; Simberloff 1979; Nobel 1981; Ehleringer 1984; and Nobel and Franco 1986).

Due to the presence of localized monospecific grass patches on Signal Hill, seedling establishment experiments were also conducted to investigate what was responsible for segregated distribution. Phillips and MacMahon (1981) purported that segregated communities may develop due to environmental patchiness, limited seed dispersal and vegetative reproduction. Thus I was able to test these ideas.

Fire is one form of disturbance that is known to play an important part in modifying the structure of communities. It has also been a factor determining vegetation structure and composition on Signal Hill. Thus I studied the effects of fire on production and flowering phenologies.

Grasses of concern in this experiment were Hyparrhenia hirta (C_4), Merxmuellera disticha (C_3) and Themeda triandra (C_4). Other common grasses which occur on Signal Hill are two introduced species, Avena barbata (C_3) and Briza maxima (C_3), and three indigenous species, Eragrostis curvula (C_4), Ehrharta calycina (C_3) and Festuca scabra (C_3). These grasses occurred opportunistically in spaces created by fire, or any form of disturbance. They were, therefore, not considered suitable experimental candidates. Some shrubs like Rhus lucida, and

other Renosterveld dominating shrubs, are also locally dominant on Signal Hill. Most, if not all of those shrubs, are regarded as increaser overstorey species which may eventually outcompete the grass community unless management practises to maintain a mixed grass/shrub are employed (De Jager 1985-unpublished).

1.1: STUDY SITES: (SEE CHAPTER 3)

The study area was Signal Hill, Cape Town (Altitude: 300-350m, latitude: $33^{0}54'$ and longitude: $18^{0}23'$). The study site was chosen for the presence of H. hirta, M. disticha and T. triandra associations, the accessibility and proximity of the site to a representative weather station (Kloofnek), which, however, only keeps limited weather records.

All except one of the vegetation patches are known to have burned last in 1975. One patch on the west-facing slope had the last fire late in February 1988. Most open spaces on the February 1988 burned patch were found to be occupied by annual "opportunists" about six months after fire. In the following year, 1989, the annual "opportunists" were substituted by shrubs. Experimental sites were established on both the east- and west-facing slopes. Both the two areas on the two slopes (east- and west-facing slopes) considered for analysis were each about 500m x 1500m, and the plots used for the different facets of this study were randomly located in the two areas. All sample sites were located on the mid- and upper-elevations of the sites.

The climate of the area is typically mediterranean. For temperature, precipitation and relative humidity, data for City Hospital station - Cape Town was considered suitable to represent Signal Hill (see Tables 1.1a, b and c below). Most of the annual total falls in winter and little, falls in spring and summer. Local topography clearly plays an important role in influencing temperature and precipitation.

Soils at the two sites seemed heterogeneous because of discrete monospecific and mixed stands of grasses and shrubs on both the slopes.

Table 1.1a: Relative humidity for Cape Town - City Hospital for the period 1951 - 1966

MONTH/MAAND	AIR TEMPERATURE LUGTEMPERATUUR in °C						RELATIVE HUMIDITY % RELATIEWE VOCHTIGHEID								
	AVERAGE DRY-BULB TEMPERATURE AT ... GEMIDDELDE DROËBOL TEMPERATUUR OM ...			AVERAGE WET-BULB TEMPERATURE AT ... GEMIDDELDE NATBOL TEMPERATUUR OM ...			08H00			14H00			20H00		
	08H00	14H00	20H00	08H00	14H00	20H00	Ū	U_s	U_a	Ū	U_s	U_a	Ū	U_s	U_a
P	9			9			9	9	9						
1	19.4			16.0			69	72	65						
2	19.0			16.5			77	89	66						
3	17.3			15.1			78	83	72						
4	15.3			13.7			83	91	77						
5	13.6			12.2			84	90	79						
6	12.3			10.7			80	83	74						
7	11.5			10.1			83	89	78						
8	12.2			10.5			79	87	71						
9	13.9			11.8			76	80	71						
10	15.4			13.1			76	89	64						
11	17.9			15.2			74	90	61						
12	19.1			15.8			69	77	65						
A	15.6			13.4			77								

NO 0020/744 2 CAPE TOWN - CITY HOSPITAL

φ33°54'S λ18°25'E HT 18 M PERIOD/TYDPERK 1951 — 1966

Table 1.1b: Temperature for Cape Town - City Hospital for the period 1905 - 1966

LUGTEMPERATUUR IN °C / AIR TEMPERATURE IN °C																												
MAAND/MONTH	GEMIDDELDES VAN MEANS OF								UITERSTES EXTREMES								GEMIDDELDE TEMPERATUUR AVERAGE TEMPERATURE OM/AT			FREKWENSIES FREQUENCIES GEMIDDELDE AANTAL DAE MET WAARDES AVERAGE NUMBER OF DAYS WITH VALUES									
	DAAGLIKSE MAKS DAILY MAX	DAAGLIKSE MIM DAILY MIN	MAX+MIN / 2	SPELING RANGE	HOOGSTE MAANDELIKSE T_x HIGHEST MONTHLY T_x	LAAGSTE MAANDELIKSE T_x LOWEST MONTHLY T_x	LAAGSTE MAANDELIKSE T_n LOWEST MONTHLY T_n	HOOGSTE MAANDELIKSE T_n HIGHEST MONTHLY T_n	HOOGSTE HIGHEST		LAAGSTE LOWEST		LAAGSTE LOWEST		HOOGSTE HIGHEST		08H00	14H00	20H00	T_x				T_n			
	T_x	T_n	$\frac{T_x+T_n}{2}$	T_x-T_n					T_x	DAT.	T_n	DAT.	T_n	DAT.	T_x	DAT.				>35	>30	<17.5	<10	>20	<5	<0	<-2.5
NO 0020/744 2 CAPE TOWN - CITY HOSPITAL φ33°54'S λ18°25'E HT 16 M TYDPERK/PERIOD 1905 – 1966																												
P	15	15	15	15	35	35	15	15	60		60		15		15		9			15	15	15	15	15	15	15	15
1	26.8	15.8	21.3	10.9	35.4	11.7	20.6	20.1	40.5	66/29	5.1	23/17	17.0	61/28	25.5	66/29	19.4			0.9	5.4	0.1	0.0	0.7	0.0	0.0	0.0
2	26.2	15.7	20.9	10.6	34.9	11.9	20.2	19.4	39.9	24/14	7.6	28/28	17.5	66/18	24.2	55/11	18.9			0.5	4.1	0.0	0.0	0.4	0.0	0.0	0.0
3	24.8	14.8	19.8	10.0	34.1	11.1	18.9	18.2	38.9	45/24	8.2	28/30	16.8	66/24	21.0	63/09	17.3			0.2	2.4	0.3	0.0	0.2	0.0	0.0	0.0
4	21.8	13.1	17.5	8.7	32.5	9.1	16.5	17.0	39.4	25/01	4.0	53/09	14.4	59/29	22.0	62/07	15.3			0.2	1.0	2.8	0.0	0.1	0.0	0.0	0.0
5	19.2	11.5	15.3	7.7	27.9	7.0	15.0	14.9	35.3	32/03	4.6	23/19	13.6	59/14	17.0	64/28	13.6			0.0	0.1	9.4	0.0	0.0	0.0	0.0	0.0
6	17.9	10.3	14.1	7.7	25.0	5.9	13.5	14.5	29.8	12/02	1.9	28/07	11.4	62/13	17.9	52/05	12.3			0.0	0.0	15.7	0.0	0.0	0.1	0.0	0.0
7	17.3	9.6	13.5	7.7	24.3	5.4	13.0	12.7	29.8	27/30	1.1	08/03	11.1	52/25	14.5	61/13	11.5			0.0	0.0	19.0	0.0	0.0	0.1	0.0	0.0
8	18.0	9.9	13.9	8.1	26.0	5.5	13.2	13.2	32.7	18/24	1.9	26/25	11.6	57/02	16.0	58/13	12.2			0.0	0.0	17.5	0.0	0.0	0.1	0.0	0.0
9	19.3	11.1	15.2	8.2	27.7	6.5	14.7	14.7	35.0	60/15	4.0	15/12	13.6	61/05	20.0	53/01	13.9			0.0	0.5	10.4	0.0	0.0	0.0	0.0	0.0
10	21.0	12.2	16.6	8.8	30.0	8.0	15.7	15.8	35.3	15/31	5.6	61/09	13.6	57/03	18.4	63/28	15.4			0.0	0.5	5.1	0.0	0.0	0.0	0.0	0.0
11	23.7	13.9	18.8	9.7	32.2	9.6	17.7	17.5	37.9	27/25	6.7	24/15	15.4	54/07	20.0	54/12	17.9			0.0	1.9	0.5	0.0	0.0	0.0	0.0	0.0
12	25.2	15.0	20.1	10.2	34.1	13.3	19.4	19.0	39.4	60/13	7.3	31/30	17.0	53/22	24.0	60/13	19.1			0.4	3.0	0.1	0.0	0.3	0.0	0.0	0.0
A	21.8	12.7	17.3	9.0	30.3	8.7	16.5	16.4	40.5	1966	1.1	1908	11.1	1952	25.5	1966	15.6			2.1	18.7	80.5	0.0	1.7	0.2	0.0	0.0

Table 1.1c: Precipitation for Cape Town - City Hospital for the period 1951 - 1966

NO 0020/744 2 CAPE TOWN - CITY HOSPITAL φ33°54 S λ18°25 E HT 16 M PERIOD/TYDPERK 1951 — 1966

MONTH/MAAND	PRECIPITATION IN MM / NEERSLAG IN MM: AVERAGE GEMIDDELD Σ	MAX IN 24 HRS / MAKS IN 24 UUR: MM	MAX IN 24 HRS / MAKS IN 24 UUR: DAT	HIGHEST MONTHLY MAX AND DATE / HOOGSTE MAANDELIKSE MAKS EN DATUM: Σ.	HIGHEST MONTHLY MAX AND DATE / HOOGSTE MAANDELIKSE MAKS EN DATUM: DAT	LOWEST MONTHLY MIN AND DATE / LAAGSTE MAANDELIKSE MIN EN DATUM: Σ.	LOWEST MONTHLY MIN AND DATE / LAAGSTE MAANDELIKSE MIN EN DATUM: DAT	FREQUENCIES / FREKWENSIES — NO OF DAYS WITH: / AANTAL DAE MET: PRECIPITATION ≥0.1MM: AVERAGE GEMIDDELD	PRECIPITATION ≥0.1MM: MAXIMUM MAKSIMUM	PRECIPITATION ≥0.1MM: MINIMUM	NEERSLAG ≥1.0MM: AVERAGE GEMIDDELD	NEERSLAG ≥1.0MM: MAXIMUM MAKSIMUM	NEERSLAG ≥1.0MM: MINIMUM	≥10MM: AVERAGE GEMIDDELD	THUNDER DONDER: AV GEM	HAIL HAEL: AV GEM	SNOW SNEEU: AV GEM	FOG MIS: AV GEM	CLOUD COVER / WOLKBEDEKKING 0-8 N: 08H00	14H00	20H00
P	15	15		15		15		15	15	15	15	15	15	15	10	10	10	10	9		
1	11	21	1963/18	41	1961	0	1955	3.3	8	0	2.3	7	0	0.1	0.1	0.0	0.0	1.2	2.3		
2	24	54	1955/18	108	1955	0	1963	3.8	7	0	2.8	7	0	0.6	0.0	0.0	0.0	0.6	3.0		
3	18	40	1962/24	50	1962	0	1964	4.6	10	1	3.2	7	0	0.3	0.4	0.0	0.0	2.4	3.0		
4	47	61	1959/11	152	1953	9	1961	8.1	16	3	5.8	13	1	1.3	0.3	0.0	0.0	1.4	4.1		
5	78	50	1951/23	202	1954	9	1963	11.3	23	3	8.4	18	3	2.8	0.3	0.0	0.0	1.8	5.2		
6	78	35	1952/20	166	1951	20	1959	11.4	21	6	9.2	18	4	3.2	0.0	0.1	0.0	1.6	4.7		
7	71	30	1956/17	161	1954	15	1958	10.4	17	5	8.6	15	1	2.4	0.2	0.0	0.0	0.7	5.1		
8	71	38	1952/04	117	1952	25	1960	12.5	17	9	9.6	16	6	2.8	0.1	0.3	0.0	0.6	5.0		
9	34	33	1952/27	112	1952	12	1960	8.5	13	2	6.6	13	2	0.8	0.2	0.0	0.0	0.6	4.6		
10	38	35	1962/07	108	1957	10	1963	8.1	15	4	5.2	11	3	1.0	0.0	0.0	0.0	0.7	4.2		
11	19	33	1963/01	54	1963	0	1960	4.6	9	1	3.2	6	0	0.6	0.2	0.1	0.0	1.2	3.8		
12	11	19	1956/26	38	1956.	0	1958	3.8	8	0	2.6	7	0	0.2	0.0	0.0	0.0	0.7	3.0		
A	500	61	1959	690	1954	321	1960	90.4			67.5			16.1	1.8	0.5	0.0	13.5	4.0		

CHAPTER 2

2.0: LITERATURE REVIEW

2.1: (a) THE BOTANICAL LITERATURE

The Cape flora is considered extremely old, and distinct from other floras, and at the same time complex within itself. Moll and Jarman (1984) and De Jager (1985-unpublished) have argued that Cape Fynbos is a heathland whose occurrence is a function of soils poor in available nitrogen and phosphorus.

(b) (i) THE ECOLOGICAL CONTEXT

Soil associated with renosterveld following (Moll et al. 1984) is restricted to fine-grained soils which are generally more fertile than those on which fynbos grows. Local soils are derived from shales of the Malmesbury and the Bokkeveld Groups, and the Klipheuwel formation, as well as Cape Granites.

(ii) PHYTOGEOGRAPHIC AFFINITIES OF RENOSTERBOS

Elytroppapus rhinocerotis is reportedly the dominant species in this vegetation type, which lacks a consistently present ericoid (Boucher 1982) or restioid and proteoid element (Taylor 1978; cited in Boucher and Moll op. cit: 243).

(iii) GRASSES IN THE RENOSTERVELD

Hyparrhenia hirta (C_4) and Themeda triandra (C_4) are reported (see De Jager 1985-unpublished) to have been significant components of renosterveld. Merxmuellera disticha (C_3) is claimed to have been observed occurring on stony hills (De Jager 1985-unpublished).

(c) HISTORICAL BACKGROUND

Many authors have postulated that the present state of renosterveld is anthropogenic (in De Jager 1985-unpublished). Acocks (1953) and Boucher and Moll (1981) note that in the past rich swards of both H. hirta and T. triandra predominated in the renosterveld. Many other authors (also in De Jager 1985-unpublished) shared similar opinions with the three quoted previously (under this same section).

2.1.1: INTERACTION

Despite a long history of research on grasses in South Africa, remarkably few studies have been done on competition between different grass species. A single unpublished M.Sc. (Mathews 1984) seem to be the only work available on grass competition in South Africa.

2.1.2(a): SPACING PATTERN

Spatial patterning has been a subject of major concern to ecologists. Three types of distributions or patterns have been distinguished; random, aggregated and regular (Pielou 1959; 1962; Yeaton and Cody 1976; Phillips and MacMahon 1981; Dayong 1989).

random distribution of populations or communities is concluded if the position of each individual plant is independent of all the others,

aggregated distribution occurs if there is a tendency for individuals of the species of populations or communities to occur in clumps, and

regular distribution is assumed when the individuals are more regularly distributed than they would if they were distributed according to chance.

The most common method ecologists employ to detect spatial arrangements of populations/communities is nearest-neighbour

analysis which was popularized by Clark and Evans (1954). Simberloff (1979) quoted Clark and Evans' technique, as well as subsequent efforts, as assuming points being infinitesimal, and since biological entities have finite sizes, one might wish to know how to "correct" a nearest-neighbour statistic based on points to allow its use in determining whether an observed arrangement of circles or other geometric bodies with finite area is random. Pielou (1961) is the only one to have examined nearest-neighbour relations for finite circles rather than points. Her results were however contentious because they do not allow one to know whether one's observed configuration of circles may be construed as random (Simberloff 1979).

To deduce amongst the three types of distributions, Pielou first used the variance/mean ratio (Greig-Smith 1957) as test statistic and the associated standard normal variate to test for its significance. Her findings were that, depending on the density and range of permissible circle size, if one interpreted the variance/mean ratio as one would have for points, one could observe clumped, random and overdispersed (regular) arrangements, even though the placement algorithm is clearly random. Further details of Pielou's variance/mean ratio test are outlined in Simberloff (1979). A chi-square test has also been utilized to deduce pattern in populations/communities.

How Clark and Evans (1954) evaluated a dispersion index (R) for populations/communities is detailed in Simberloff (1979). Dispersion index (R) was used to determine the significance of departure from randomness towards aggregation or regularity, i.e. $R = \bar{r}_a/\bar{r}_e = (\Sigma r)(2\sqrt{\rho})/n$, where $\bar{r}_a$ = the mean observed nearest-neighbour distance (r/n), r = measured distance to nearest-neighbour and n = number of such measurements, and $\bar{r}_e$ = the expected mean nearest-neighbour distance given random dispersion $(1/2\sqrt{\rho})$, where ρ = density and is expressed as number of individuals per unit area. The density estimated is obtained from the quadrat results. The advantage of such distance-based measures of dispersion is that the scale of the pattern examined is not restricted to any particular quadrat

size (Phillips and MacMahon 1981). Dayong (1989) cited some authors such as Pielou (1977), Greig-Smith (1983) and Kershaw and Looney (1985) as having utilized other methods to deduce spatial pattern in populations/communities.

The usual approach employed by plant ecologists when attempting to detect and analyse the spatial pattern in populations/communities is a nested analysis of variance of data from transects or grids (Dayong 1989). However, it suffers from the drawback of arbitrariness in the choice of quadrat size and starting point (Usher 1969; Ripley 1978). Dayong (1989) quoted authors such as Ripley (1977, 1981) and Diggle (1983) as having developed more sophisticated techniques for the analysis of mapped point patterns. Dayong's method of detecting departure from randomness in plant communities is based on the theoretical distribution of the length between successive ordered points in unit interval, and he, in the same paper, argued that this method is more powerful for at least certain patterns. Mathematical details, examples and discussions on the method are detailed in his paper (Dayong 1989).

There have been controversies however on the use of pattern to infer competition, e.g. "distance sampling by taking the distance from a random individual to its nearest-neighbour will obscure any but very local effects and is not necessarily informative about competition" Hill 1973. Meagher and Burdick (1980) have also mentioned that this method may produce erroneous results which may lead to assignment of statistical significance where none exists. They pointed out that there have been violations of chi-square test assumptions in nearest-neighbour frequency analysis which they believe could cause major alterations in interpreting such analyses.

All in all the methods discussed have, over time, played a key role in unlocking the doors to our understanding the patterns in which populations/communities of plants could be arranged in nature.

(b): MECHANISMS: DISTRIBUTION PATTERNS OF SPECIES

Regular distribution of plants has been reported in desert populations/communities (Macnaughton and Wolf 1979; Smith 1980; Nobel 1981). One of the mechanisms that is assumed to generate this pattern is root competition for water, with consequent density-dependent mortality (King and Woodell 1973; Yeaton and Cody 1976; Smith 1979).

Moderately persuasive is the fact that seedlings or juveniles show a clumped distribution pattern. That aggregated populations/communities are observed where reproduction is vegetative has been reported (Phillips and MacMahon 1981). But that type of pattern vanishes as plants become medium-sized. Medium-sized plants tended towards random arrangement, and larger ones tended to regular pattern. Anderson (1970) in a number of varied sites in some Australia dryland plant communities, asserted that younger plants are clumped and that the pattern disappeared as they grow larger and exerted more influence on each other. He concluded that whilst the original establishment may be subject to quite strong environmental control, subsequent development of community pattern (in terms of density) is influenced to a considerable extent by the plants themselves. For an example, as soil water availability becomes scarce, plants will tend to extend their roots towards unexploited soil volumes in the immediate vicinity. In so doing, especially in overcrowded forests, weaker competitors will be deprived of moisture in their immediate root zones, and thus weakened and eventually be excluded from populations/communities. The processes are of course quite gradual, and depending on the sizes of the remainders in populations/communities, plant dispersion pattern will trend from being aggregated to being random, and eventually to uniformity (regularity). Greig-Smith and Chadwink (1965) found a diminution of aggregation with increasing shrub sizes, but confirm no testimony of uniform pattern. Beals (1968) found that desert shrubs in Ethiopia generally exhibited regular dispersion especially in areas of high density. He suggested

some form of competition in the plant spacing. Many studies, some in Phillips and MacMahon (1981), corroborated the prevalence of regular distribution as plant sizes increase from small to medium, and eventually to larger sizes.

Which ever kind of distribution pattern is observed in populations/communities, the crux of the matter is that both abiotic and biotic factors are "causers". The distribution of plants in unfavourable environments has been for generations ascribed to the influence of physical factors (MacDougal 1908; Spalding 1904; Canon 1911; Turnage and Hinckley 1938). Other environmental factors such as temperature, nonequilibrium phenomena (e.g. fire- referred earlier), etc. are also known to play an important role in patterning the world's plant communities.

2.1.3: REMOVAL EXPERIMENTS

Removal experiments involve isolation of any particular individual species by removing its nearest-neighbour(s) to confirm the existence of competition. This method depends on one's aims and also what one understands as a suitable way of isolating individuals: it might be to establish whether the species are competing for water, nutrients, volume of space, etc. Clipping, or entire removal of the aboveground parts of nearest-neighbour individuals, or excavating all the neighbouring individual(s), are some of the methods that can be utilized.

This technique (removal experiments) has received wide application. Fowler and Antonovics (1981[I]), Fowler 1981[II], 1982, 1984) applied this technique to assess effects of competition on the cover of each species, weight and number of flowers per plant. Robberecht et al. (1983), Ehleringer (1984), Baruch et al. 1985 and Eissenstat and Caldwell (1988) utilized this same procedure in their studies on the effects of removals on water relations, growth productivity, reproduction and photosynthetic responses of grasses and shrubs; enhancement of

all the aspects investigated were confirmed. Ball and Hayne (1952), Fonteyn and Mahall (1981), and Nobel and Franco (1986) have reported the success of removal experiments in ascertaining some competitive processes. Simberloff (1979), Pacala and Silander (1985), Pacala (1986), Penridge and Walker (1986), Cox (1987), Firbank and Watkinson (1987) all used this technique, presumably because it is more consistent for botanical analysis. Yeaton (1988-unpublished) after a series of removal experiments at Mniszechi Vlei of the Namib Dune grasslands, Namibia, found no significant difference between the control and the experimental treatments in the number of individual tillers or whole plants dying over the experimental period. Significantly more of the experimental S. sabulicola were found increasing their leaf number than those of the controls. Removal experiments were also conducted in which the removal of all neighbouring plant biomass within a 2m radius of individual Schizachyrium scoparium bunches resulted in a 3.8 fold increase in the biomass of S. scoparium bunches (Tilman 1989). Fowler (1986) in a study to examine the extent to which plant population dynamics are affected by density-dependent processes in six out of seven quadrat sets, found that plants in adult removal quadrats were on average larger than plants on the control quadrats; no competition by seedlings against adults was observed.

2.1.4: PHENOLOGY

Phenology has been defined as the study of recurring biological events, which involves both qualitative and quantitative measurements (Pierce and Cowling 1984). In their study of fynbos, renosterbos and subtropical thicket in the south eastern Cape, Pierce and Cowling (1984) concluded that soil type had minimal effect on the phenophases of species growing on them.

They found that C_3 grasses grew most actively in the cool wet seasons, and C_4 grass species showed either a summer growth

season or an additional cooler growth season; they found that the former species (C_3 grasses) do not occur westwards in the winter rainfall region while the latter (C_4 grasses) do. They explained phenophase pattern in terms of ecophysiological factors, but biological and historical factors were also considered. The following are the phénophases observed: obvious manifestations like shoot elongation, leaf initiation, development, preflowering (budding), full flowering (open flower), and unripe and ripe fruiting/seeding, leaf yellowing, prior to and including abscission.

Low temperature was found to defer flowering in the grass Aristida contorta (which has been reported to germinate in the warm season) (Mott and McComb 1975).

In their work on phenology of drought-deciduous shrub Lotus scoparius, Nilsen and Muller (1981) found that phenological progressions of leaf production, leaf composition, shoot elongation, lateral branch production and flowering on even-aged stands of this species were correlated with factors such as temperature, relative humidity, soil moisture, plant water relations, and photoperiod. These correlations, they asserted, were determined during both a characteristic and an uncharacteristic growing season for this mediterranean-climate region.

2.1.5: SEEDLING ESTABLISHMENT/TRANSPLANT EXPERIMENTS

Seedling establishment is a situation whereby individual organisms (seedlings/adult plants) are removed from their original areas, and introduced into new areas, to observe after a certain specified time (period) the effects on survivorship, fecundity, and reproduction. According to Krebs (1978) these kinds of experiments, require to be followed for at least one complete generation since some organisms are known to survive without reproducing. Krebs (1978) in a chapter, methods for analyzing distributions, gives a terse explanation on what the transplant experiment is all about.

Amongst other things, he mentions how one could answer the question of what limits distribution. He argues that it can be achieved by first determining whether the limitation of distribution comes from the inaccessibility of any particular area, plot, etc to individual organism(s) established or transplanted. Transplant experiments, he maintained are contributory to determining the source of limitation. His two hypothetical outcomes of the transplant experiment that dictate where to go next are as follows:

> if the outcome of transplant experiment is successful, the interpretation is that distribution is limited because either the area is inaccessible or because the organism fails to recognize the area as suitable living space; and if the outcome of the transplant experiment is unsuccessful, the interpretation is that distribution is limited either by other species or by chemical and physical factors. If a transplant is found successful, the assumptions are that it indicates the potential range of a species is larger than its actual range.

Pielou (1960, 1961, 1962), Phillips and MacMahon (1981) observed clumped patterns of vegetation and ascribed them to environmental patchiness, limited seed dispersal and vegetative reproduction. Ecologists offer many different reasons for the outcome of transplant/seedling establishment experiments: date of transplant, planting density, the species transplanted, fine-scale adaptation, light intensity, seed size, shading effect, site of transplant, soil moisture, soil type, etc (Kramer et al. 1952; Grime and Jeffrey 1965; Friedman 1971; Doust 1981; Burton and Mueller-Dombois 1984; Waser and Price 1985; Winn 1985; Fowler 1986; De Jong and Klinkhamer 1988; Fowler 1988; Klinkhamer and De Jong 1988).

2.1.6: FIRE AND OTHER FORMS OF NONEQUILIBRIUM PHENOMENA

Fire has played a role in shaping the world's grasslands and forests. Attempts to eliminate it have introduced problems as serious as those created by accidental conflagrations (Cooper 1961). The fact that fire has been an issue of major concern in structuring plant populations/communities is well known. The early Portuguese explorers have been cited as stating that the interior of South Africa, from the Cape to Natal, was covered by a pall of smoke due to veld burning, and called the country "Terra dos Fumos". Roux (1969; quoted in Scott 1970) stated "we may believe with some assurance that the burning of veld in winter was a common occurrence long before the coming of the Europeans". Various reasons for veld burning are known. The Bushmen used fire to provide green grass for game which they could then hunt, Africans burned veld to provide nutritious grazing for their livestock, and honey hunters often started fires which then spread over large areas.

How many fires are caused by lightning and intense heat remains unknown. Komarek (1966, in Scott 1970) discovered from foresters' reports in the United States that 90% of all American woodland fires were set by lightning, and these ran into thousands per annum. Many cases concerning veld fires in this country have been reported (Scott 1970). Scott (1970) quoted farmers as claiming that it is impossible to farm in the sour veld without veld burning. Roux (1969, in Scott 1970) has been reported as having stated (Sauer 1956) that the origin and preservation of grasslands is due, in the main, to burning and...they are in fact great and, in some cases, ancient cultural practices.

In accounting for fire as a natural factor of the environment Scott (1970) referred to grassland areas adjacent to savanna areas such as those in the Eastern Cape. He argued that fire has played a significant role in keeping those areas as grasslands. Scott further argued that it was with the insistence of Soil Conservation Committees that veld burning is a wrongful practise and should be stopped, that a very marked

encroachment of bush into areas which were pure grasslands ensued. Fire is also "known" to have kept many mountainous areas of the Eastern Province free of fynbos for many years, and that it was after the prohibition of veld burning that fynbos started encroaching these areas (Scott 1970). In the sour veld areas, fire has always been a most important factor in the removal of waste material left from the previous season. Where there was selective grazing or accumulation of old grass, as the result of a rest from grazing, the old grass was burned off at the beginning of the next season to give a clean sward (Scott 1970). Scott further argues that if the old grass were not removed it became moribund, and within a couple of seasons it died out making way for weeds and plants useless for grazing. From the above it appears reasonable to view fire as one of the important effective factors in maintaining and establishing productive grasslands.

Other reports on the role of fire are that in open country fire favours grass over shrubs (Cooper 1961). Notwithstanding shrubs known to grow vigorously immediately after burning, their living tissues stand well above the ground, fully exposed to fire, with the result that repeated burning will keep them rather small. Woody plants are also known to be more susceptible to fire as compared to grasses (Cooper 1961). Perennial grasses, for example produce seeds abundantly one or two years after establishment, whilst most woody plants require several years to reach seed-bearing age. There are nonetheless controversies as to the role of fire in maintaining grasslands. Some biologists believe that a substantial portion of North American grasslands owe their origin and maintenance to fire (Cooper 1961). Others argue that climate is the main deciding factor, whilst fire had little influence (Cooper 1961). Some areas like the Great Plains of North America have been used to invalidate the belief that grasslands owe their origin and maintenance to fire. In other places, for example the grass covered Palouse Hills of the south-eastern part of the state of Washington, the soil is known unsuitable to shrub growth, although the climate is favourable (Cooper 1961). An example is

the forest of the jack pine that spread in a broad band across Michigan, Wisconsin and Minnesota (Cooper 1961).

Despite the arguments discussed above, the importance of frequent/regular burning is referred to as very important in maintaining plant populations/communities to the "optimal" status (Rethman and Booysen 1968; Downing 1974; Trollope 1974; Robinson et al. 1979; Drewes and Tainton 1981; Everson and Tainton 1984; Everson and Everson 1985; Trollope and Potgieter 1985; Barker and Williamson 1988; Everson and Van Wilgen 1988; Yeaton et al. 1988).

Another means of disturbance that formed part of the current research is removal experiments. Experiments at the Estcourt and Tabamhlope Research Stations demonstrated conclusively the need for removal of the old ungrazed grass before the next growing season. They showed that removal by mowing was much superior to burning, and that the yields from mown veld in the subsequent season were much higher than from any burned area of comparable size (Scott 1970).

Other disturbance phenomena beyond the limits of this study, such as cattle grazing (Kydd 1964; Noy-Meir, Gutman and Kaplan 1989), ant-mounds and animal burrows (Coffin and Lauenroth 1988), hurricanes and hoofprints (Belsky 1986), are known to play significant roles in patterning plant populations/communities. Grazing by large herbivores is generally recognized as a paramount ecological factor in grasslands, and has been suggested as an important evolutionary force (Harper 1969, 1977; Whittaker 1977; McNaughton 1979, 1984; Mack and Thompson 1984). Some studies on grasslands suggested the importance of within-community patch-producing disturbances on spatial pattern, and on the persistence of species able to utilize small, relatively short-lived patches, e.g. ant-mound and animal burrows (Platt 1975; King 1977; Hobbs and Mooney 1985; Loucks et al. 1985).

2.2: MECHANISMS OF COMPETITION

2.2.1: GROWTH, PRODUCTION AND REPRODUCTION

Growth, production, reproduction, etc. are geared to both biotic and abiotic factors. For instance, optimal light intensities, temperature, water etc. are indispensable commodities for plants to photosynthesize optimally and efficiently, thus producing enough food for growth and establishment. Positive relationships between water (soil water availability) and growth, production, reproduction, etc. have been severally confirmed (Ehleringer, Bjorkman and Mooney 1976; Ehleringer and Mooney 1978; Ehleringer 1980; Ehleringer 1984; Ehleringer and Cook 1984; Knapp 1984; Eissenstat and Caldwell 1988). Nonequilibrium phenomena like veld burning (referred earlier), have been found and recommended factors that stimulate growth, production, reproduction, etc. Competition has been proved to affect plant life processes negatively. One example is when one plant affects another plant allelopathically. Whilst in a no competition situation (e.g. where disturbance has occurred, either through removal experiments or otherwise), improvement in plant growth, production, reproduction, etc is observed. In essence any other factor, abiotic or biotic, if improperly induced inhibits proper operation in a plant's processes, thus causing negative results in the overall operation of the plants' metabolic machinery.

2.2.2: PHOTOSYNTHESIS

Photosynthesis is a food manufacturing process which involves a series of enzymatic reactions. However, in other type of plants such as C_4 that fix their carbon by reacting with the three carbon PEP (phosphoenolpyruvate) to form oxalacetate, water loss is quite restricted. Crassulacean acid metabolism (CAM) plants fix their carbon in the same way as C_4 plants, but

the process is restricted to the night. This renders those plants better adapted to semi-dry weather conditions.

Another problem known to bedevil photosynthesis (in C_3 plants) is photorespiration, i.e. oxygen interferes with the initial combination of carbon dioxide and ribulose bisphosphate (RUBP), so that instead of combining with the carbon in carbon dioxide to form two three-carbon PGA molecules, the RUBP splits to form single molecules of phosphoglyceraldehyde (PGA) and phosphoglycollate.

The three photosynthetic pathways referred to above, i.e. C_3-, CAM- and C_4-fixation pathways, are known to dictate under what conditions plants have to grow to establish efficiently (Vogel et al. 1978). In other words C_3-, CAM- and C_4-plants are found to be geographically distributed according to their respective carbon fixation mechanisms. Crassulacean acid metabolism (CAM) plants occur in semi-arid conditions, C_3 plants are found under cool temperate winter rainfall regions, and C_4 plants are dominant under warm tropical and subtropical summer rainfall conditions (Vogel et al. 1978; Ellis et al. 1980; Cowling 1983b). The photosynthetic temperature optima and photosynthetic light intensity optima for C_3 plants are quite low, whilst those for C_4 plants are quite high. These, therefore, render C_4 plants more competitive relative to C_3 under high temperatures, high light intensities, and also under low carbon dioxide concentrations, whilst the converse is favourable for C_3 plants (Black 1971; Bjorkman 1975). In essence, C_3 plants would be displaced from a community under environmental parameters that are favourable to the efficient performance of C_4 plants and vice versa (Ehleringer and Bjorkman 1977).

2.2.3: WATER RELATIONS

Under field conditions leaf water deficit develops when water loss through evapo-transpiration exceeds leaf water uptake

(Hsiao 1973; Roberts and Knoerr 1977). Stomatal behaviour and cell wall extension are both turgor phenomena, and may be related to leaf turgor potential (Clelland 1971; Penning de Vries 1972; Hsiao 1973) while the capacity for leaf tissue to gain substrate water is related to the depression of osmotic and matric potentials below the water potential of the substrate.

Both C_3- and C_4-plants, as highlighted in discussion on photosynthesis, differ in their geographical distribution, with C_3 plants probably competitively advantaged under cool, moist places and C_4 plants favoured under warm semi-dry places (Vogel et al. 1978; Ellis et al 1980). C_4 plants have evolved an efficient photosynthetic mechanism of water conserving under dry conditions, whilst C_3 plants have not. Carbon gained/water lost is greater in C_4 plants than in C_3 plants, thus resulting in C_3 plants being readily outcompeted by C_4 plants under low water conditions.

CHAPTER 3

3.0: STUDY SITES AND SPECIES

3.1: GENERAL

With the strong tenet that "vegetation changes according to the way it is treated," I share with Sparrman (quoted in Smith 1966), Marloth's hypothesis in 1908 that the renosterbos-dominated plant community termed renosterveld is an artificial one which results from a harsh disturbance regime (Levyns 1930).

3.1.1: OTHER STUDIES

(a) CAPE TOWN SIDE

There is a hypothesis that the Elytroppapus renosterbos dominated plant community termed renosterbos is an artificial one resulting from a harsh disturbance regime (frequent fire, overgrazing, wood removal and the elimination of most of the indigenous fauna)(Mitchell 1922, in De Jager 1985-unpublished). This hypothesis has been further elaborated by Eugene J. Moll (pers. comm.) and Tansley (1982) by further adding that renosterveld had a much greater grassy component which was eliminated, or severely reduced, by human impact during historic times. The hypothesis tested in De Jager (1985-unpublished), is that renosterveld, given a more natural disturbance regime, would undergo a succession towards something akin to its former grassy state.

The vegetation on Signal Hill was called "sclerophyllous bush" (a general term for the vegetation of the western Cape at that time it seems) by Mitchell (1922). However, it is now called coastal renosterveld (Tansley 1982).

However, it is interesting to note Theron's (1984) idea that "the seeds of renosterbos were probably transported to this

region in the Cape Peninsula by man (or were windblown)". He bases this assertion on the absence of Renosteria from the Peninsula. Be this as it may, since at least 1919, renosterbos has been established on Signal Hill (De Jager 1985-unpublished). Levyns (1952) records that it displays a definite preference to stiff clays here, which "is blown with almost diagrammatic precision as below Lion's head, where granite replaces slate, the soil is coarse and the Renoster Bush no longer dominates the scene".

The soil on most of Signal Hill is fine in texture, being derived from Malmesbury Shales. Results of soil samples analysed (from De Jager 1985-unpublished) are summarized in Tables 3.1.1(i) & (ii):

Table 3.1.1(i): Soil sample analysed by George Thompson

	Signal Hill	
	Cape Town Side	Seapoint side
pH	4.6	4.7
Resistance in Ohms	1420	1700
Available phosphates ppm	1	2
Total cations in milli-equivalent percentage	5.82	7.36
Cation exchange capacity in milli-equivalent percentage	8.04	7.65
Sodium in milli-equivalent percentage	0.82	1.83
Potassium in milli-equivalent percentage	0.07	0.65
Calcium in milli-equivalent percentage	3.34	3.79
Magnesium in milli-equivalent percentage	1.64	2.09
Percentage total Nitrogen	0.119	0.141

Table 3.1.1(ii): Phosphorus determination

	Phosphorus in microgram/gram dry mass of soil	
	Available	Total
Signal Hill-Shale on Cape Town side	5.93	206.36
Signal Hill-Shale on Cape Town side	4.86	204.54
Signal Hill-Shale on Seapoint side	10.20	133.20
Lion's Head Granite on Seapoint side	2.80	137.57

The fauna reported to have occurred in the area by Marshall, one of the local residents living at the foot of the valley on the Cape Town side (De Jager 1985-unpublished), are tortoises, small buck, guinea fowl, francolin and lynx (reported by three different people). During my work on the site I saw mice, tortoises and mole-rat mounds.

"At Signal Hill the vegetation is very depauperate and the ground eroded due to frequent fires, trampling, litter and large alien infestations" (Tansley 1982:23). However, Tansley noted that the site has high educational potential as part of the Table Mountain Nature Reserve.

3.1.2: HUMAN IMPACT ON VEGETATION

The four sources of impact which pertain to the mid-1900's, besides total destruction of the vegetation by building activity around the hill, quarrying, road building and afforestation on the hill, are a short-interval fire regime, stock grazing, fire wood collection and invasion by alien plants. The elimination of much of the fauna in earlier times and probably the removal of larger trees for timber has affected the present state of the vegetation (De Jager 1985-unpublished).

3.1.3: FIRE

Accounts in (De Jager 1985-unpublished) are that on the Peninsula, "the lengths of periods between burning the same area were perhaps, on the average, three years, but some luxuriant types of vegetation, particularly on marshy soils, would be burnt again within one year". Mitchell (1922) emphasised that frequent burning was necessary for the provision of grazing for livestock and of fire wood for poor people in the area. But these practises were reportedly short-term, i.e. Levyns (1924) observed that three years after the

1919 fire on Signal Hill, " the renoster bush had taken possession of the hillside, and, in doing so had ousted the grasses and other plants suitable for grazing (1924: 247)".

From information assembled by Liz Ashton (pers. comm.) the fire history for Signal Hill is:

up to 1950's- general fire regime consisted of regular fires, just about every summer big areas would burn both the Cape Town and the Sea Point sides.

in 1952- Levyns (1952, in De Jager 1985-unpublished) described the whole of the Lions' Rump on Signal Hill as being clothed with renosterbos. "A closer examination shows that other plants grow amongst the Renoster Bush but from a distance the renosterbush and its larger associate the Taaibos (Rhus lucida) dominate the slopes (1952)".

from 1960- there was a sudden curtailment of fires due probably to stricter law enforcement and quicker response on the part of the fire fighting agencies.

in 1969- last recorded big fire, which was started at the military camp, in a southeaster, burned up the slopes and over the top towards Sea Point, covering 200 acres.

in 1972- there was burning of another big fire.

during 1974 and 1975- lots of small grass fires consumed many hectares.

February 1988- small grass fire on M. disticha-dominated stand on ridgetop, Sea Point side - personal communication (Clive May of the Kloofnek Nature Reserve Station).

3.1.4: GRAZING

Mitchell (1922) refers to cattle grazing on Signal Hill, and thus an acceleration of soil erosion which resulted from the formation of cattle tracks. This was descriptively further researched by Liz Ashton who gathered information from Mr Watson, an 85 year old ex-council development engineer who lives in Claremont, and another informant who lives in Springbok Street - below Signal Hill.

In the pre-1900's, farmers in Oranjezicht (e.g. the van Bredas-dairy farmers) are reported having kept cattle, sheep and goats on Signal Hill; and as these disappeared from the area, people living in the Malay Quarter of Schotsekloof are reported as having kept some stock, mostly goats, intended for the Moslem feasts and celebrations. In the late 1950's and 1960's law enforcement, motivated by abattoir regulations concerning the health hazards of backyard slaughtering, phased this practise out.

3.1.5: FIREWOOD COLLECTION

Judging from Mitchell (1922), it is apparent that this was a constant impact until recent times. She described the loosening of soil following activities of wood-gatherers who did so by dragging their bundles down the hill. In this regard, it is interesting to note that Protea nitida is listed by Skead (1980) under its synonym of P. grandiflora among the many victims of the Cape's woodcutters, while Smith (1966) notes that its wood "gives an excellent charcoal for household and smithy work, and there can be little doubt that many thousands of trees must have been cut down from earliest days to supply the demand". Although he rejects this explanation in favour of the more conventional one, Smith does record the belief of firewood cutters "that the vernacular name ("waboom") was derived from the use the woodcutters made of the large growths for carting loads of wood down the slopes on which the plants grew (ibid).

3.1.6: AERIAL PHOTOS

From aerial photographs the following data were extracted by De Jager 1985-unpublished:

1935- cattle tracks were reported clearly evident. Also some signs of ploughing which may indicate an old farm.

1951- sparse vegetation reported which was attributed to recent fire. An increasingly dense growth of alien pines (e.g. Pinus pinaster) was observed.

1944- the vegetation cover on the north-facing slopes reported to be relatively sparse.

1953- indication of rather poor management reported.

1958- the first plantation of the Eucalyptus was observed at the foot of the ridge.

1968- the vegetation in the study area was mature (richly textured and dark), with a good cover. There was also mention of a fire break or some similar disturbance running down the valley.

1977- lots of the plantations seemed to have been removed.

1980- "vegetation mature-looking and with a dense cover- indicative of the long fire interval relative to the period covered by most of the other photos. A heavy infestation of pines and Eucalyptus remains on the northeast tip of Signal Hill, while Eucalyptus trees line the base".

3.1.7: ALIENS

Within the study area, Pinus pinaster, Lantana sp., Pennisetum cetaceum and Eucalyptus spp. were observed.

3.2: SIGNAL HILL: SEA POINT SIDE

Some of the general information about the Cape Town side, such as the law enforcement, farming and wood-cutting is also applicable here.

A dense T. triandra sward with a strong component of small shrubs was sampled. On the other parts H. hirta was reported dominating with odd plants of Themeda and Cymbopogon occurring. Rhus bushes were found evenly dotted throughout this grassland. Aliens such as Eucalyptus are there.

3.3: OUTLINE OF THE THREE GRASS SPECIES CHOSEN FOR STUDY.

3.3.1: (a) Hyparrhenia hirta- a perennial C_4 grass (Russell et al. 1990

(i) Habitat- often in disturbed places, also an important constituent of open grasslands (Chippindall and Cook 1976)

(ii) Flowering- from September to June (Russell et al. 1990). Inflorescence- from September to March (Chippindall and Cook 1976).

(iii) Economics- a valuable fodder grass (sweetgrass) when young, probably provides fairly good grazing when mature (Weinbrenn 1938, 1939; Weinmann and Reinhold 1946; Robinson and Potts 1950; Tainton and Booysen 1965b; Chippindall and Cook 1976; Wolfson et al. 1982; personal experience). Where common it is widely used as a good thatching grass (personal experience) and in Lesotho it is used for weaving into very large (4 to 6 m high) grain storage baskets called (sisiu) (Guillarmod 1971, in Chippindall and Cook 1976).

"The dense tufts are locally (Fauresmith) common and said to be the favourite haunts and breeding place of the bushtick" (Smith 1966, in Chippindall and Cook 1976).

(b) Merxmuellera disticha- a perennial C_3 grass (Russell et al. 1990)

(i) Habitat- characteristically a short grass of montane areas (Chippindall and Cook 1976).

(ii) Flowering- from October to May (Russell et al. 1990). Inflorescence- not known (Chippindall and Cook 1976).

(iii) Economics- none known but in certain karoo mountain veld types it is sometimes dominant (Acocks 1953); it is possibly an indicator of mismanagement leading to

encroachment by Karoo False Fynbos. Reported as an unpalatable grass (Chippindall and Cook 1976).

(c) Themeda triandra- a perennial C_4 grass (Russell et al. 1990)

(i) Habitat- reported to be a component of climax montane grasslands, and also to grow at lower altitudes, particularly in the tropics, also observed as common in woodland. It is also described as common and ubiquitous on all types of soil including shallow and wet ones (Chippindall and Cook 1976).

(ii) Flowering- from September to June (Russell et al. 1990). Inflorescence- from October to July (Chippindall and Cook 1976).

(ii) Economics- many ecologists since the early 1900's reported it a good veld cover, and a most palatable, and desirable pasture grass, and also usable for thatching (e.g. Codd 1928; Mes and Aymer-Ainslie 1935; Tainton et al. 1977; Clayton and Renvoize 1986 and Danckwerts 1987a & b), and is dominant over wide areas of southern Africa, mostly under warm/hot summer rainfall regions (Chippindall and Cook 1976; personal experience).

CHAPTER 4

4.1.0: DISTRIBUTION PATTERNS AND NEAREST-NEIGHBOUR INTERACTIONS

4.1.1: ABSTRACT

This chapter describes the competitive interactions between three perennial grasses, Hyparrhenia hirta (L) Stapf (C_4)*, Merxmuellera disticha (Nees) Concert (C_3)* and Themeda triandra Forsskal (C_4)* which coexist on the east- and west-facing slopes of Signal Hill, Cape Town.

Through quadrat sampling it was determined which of those species was most dominant relative to the other two species.

Competitive interactions were inferred from pattern analysis. In the first place, the distribution patterns of the three grasses were analysed using a dispersion index (R). In all five cases, except one, distributions tended towards regularity; the exception tended towards aggregation. Secondly, nearest-neighbour analysis was used to detect inter- and intra-specific competition. Ratios of the diameters of the smaller individuals to the distances from their neighbours showed that for individuals of the same size, both inter- and intra-specific nearest-neighbours were located at nearly the same distances. The slopes of regression lines of the combined cover versus distance for different nearest-neighbour pairs were also compared. Results indicated the relative intensity of competition among and within species. M. disticha appeared to be growing better than H. hirta, whilst T. triandra, wherever it occurred with M. disticha, appeared to be competitively stronger. As a resultant regular distribution is anticipated for the species in the long-run. In some cases, intraspecific competition was relatively more intense than interspecific, whilst in others interspecific was rather more than intraspecific. Accordingly both mixed and segregated populations are feasible, as well as the exclusion of weak competitors.

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*FOOTNOTE: The C_3 and C_4 nature of the plants was determined microscopically

4.1.2: INTRODUCTION: DOMINANCE, DENSITY AND SPECIES PATTERNING

The grass flora of the cooler, winter rainfall regions of South Africa is dominated by C_3 grasses (Vogel *et al.* 1978). Nevertheless C_4 grasses, including such essentially subtropical species as *T. triandra* and *H. hirta*, do occur in the Cape. Most C_4 grasses, such as *T. triandra* and *H. hirta* would be expected to dominate in the warmer, summer rainfall regions. However there are reports of C_4 grasses occurring in the west- and north-facing slopes of the cooler, winter rainfall areas (Cowling 1983). Cowling (1983) predicted from an analysis of physiological characteristics of C_3 and C_4 grasses that C_3 grass species would be most abundant in cool shaded sites. He found that C_3 grass cover was significantly correlated with increased post-disturbance vegetation age, low intensity grazing, high litter cover and cool, steep poleward slopes. C_3 grasses were found not to occur on the west-facing slopes in the winter rainfall region, while C_4 species did (Pierce and Cowling 1984). Pierce and Cowling (1984) found higher relative grass cover of C_3 grasses on the cooler south slopes, while C_4 grass cover was higher on the north slopes.

The original history of C_4 grass species is not entirely known, and yet some (C_4) species, such as *T. triandra*, *H. hirta*, etc are important pastorally. They are also indispensable for thatching. To maintain them efficiently, their biology (ecology, physiology, etc) should be well understood.

Photosynthetic rates of C_4 plants are generally believed to be favoured by relatively high temperatures and light intensities, while the converse is true for C_3 plants. It might therefore not be naive to argue that C_4 plants have originated in the deserts. There is evidence that C_4 grasses dominate in the warm summer rainfall regions because of their photosynthetic pathway (Ellis 1971; Teeri and Stowe 1976; Winter *et al.* 1976; Chazdon 1978; Vogel *et al.* 1978; Tieszen *et*

number of individuals of that species by the number of quadrats in which it occurred);

ii) density: defined as the number of individuals per quadrat, obtained by dividing the total number of individuals of that species in all quadrats by the total number of quadrats examined;

iii) dominance: defined as the average basal area of each species per quadrat;

iv) relative density: defined as the number of one species as a percentage of the total number of individuals of all species; and

v) relative dominance: defined as the basal area of one species as a percentage of the total basal area of all species.

The above was carried out to investigate which grass species amongst those occurring on Signal Hill were fairly abundant and dominant for subsequent analysis.

Those species which were found to be reasonably abundant in this census were considered for pattern analysis, i.e. evaluation of dispersion indices (R) and correlation coefficients (r).

Pielou (1959, 1960, 1961, 1962) and others (Yeaton and Cody 1976; Bawa and Opler 1977; Phillips and MacMahon 1981; Dayong 1989) noted that in studying the spatial arrangement of natural populations/communities of plants, three types of distributions or patterns can be distinguished: random, aggregated and regular. The individuals of a species are said to be at random if the position of each individual plant is independent of that of all the others; aggregated populations/communities are those in which there is a tendency for individuals of the species to occur in clumps; and in regular populations/communities the plants are more evenly spaced than they would be if they were distributed according to chance. Feller (1943) has noted the commonness of aggregated populations in nature, and gives two possible causes for this aggregation. On the one hand seeds may fall at random over an area, but the habitat may be non-homogeneous, thus differentially influencing the proportion germinating and thriving. The result is that the density

becomes high at some sites and low at others. On the other hand the habitat may be homogeneous, but the individual plants occur in family groups owing to the fact that they reproduce vegetatively, or by seeds with a small radius of dispersal.

According to (Greig-Smith 1957) a regular pattern would be expected to occur if the members of a population were so abundant that they competed with each other for the available space.

One approach to the study of pattern is based on nearest-neighbour distance.

All in all (Pielou 1959) recommended three distinct parameters to measure:

a) an estimate of density
b) a sample of plant-to-neighbour distances, and
c) a sample of point-to-nearest-plant distances

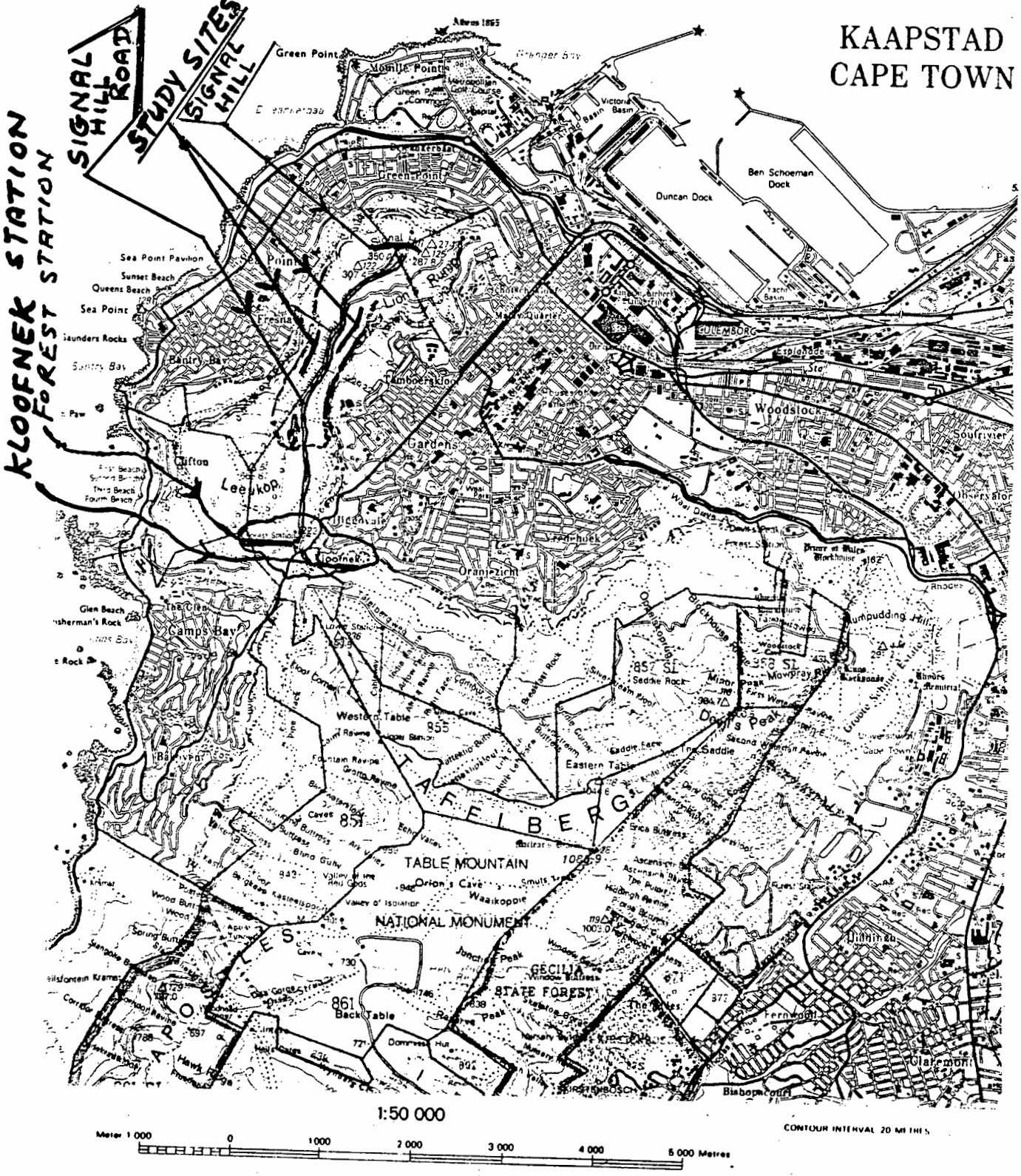
Hopkins (1954) applied a) and c) to judge whether or not the plants are randomly dispersed. Clark and Evans (1954) have devised a test based on a) and b) and their results give density, a test for non-randomness and a measure of non-randomness

My general approach for the determination of pattern is similar to that of Clark and Evans (1954).
The following questions were asked:

i) What are the distribution patterns of both C_3 and C_4 grasses on Signal Hill?; and
ii) What allows C_4 grasses to occur in relatively large numbers in some places of the Western Cape (e.g. east-, west- and north- facing slopes of Signal Hill)?

4.1.3: MATERIALS AND METHODS

Fig 4.1.3: Schematic representation of Signal Hill (Study Area)



The two slopes (i.e. east- and west-facing) considered for this study were dominated by grasses, herbs and shrubs. Sampling was by quadrat method on both the slopes. This method has been found to be more consistent for botanical analysis (Everson and Clarke 1987). The quadrats on both the slopes were placed from about ridgebottom (some 100m from the firebreak) up to the ridgetop (about 10m from Signal Hill road). The overall area sampled was about 500m x 1500m. Quadrats were randomly located by throwing a stone high up in the air and using the point it landed as the center-mark. Twenty five 1.5m x 1.5m quadrats were sampled in this manner.

The diameter of each individual of the following grass species included in the quadrat was measured: H. hirta, M. disticha and T. triandra. This was done to investigate which grass species amongst the three was dominant both in number of individuals, and area cover (i.e. in each case individual species were identified, measured and then counted). Counting was per quadrat. Each individual which had more than half its canopy cover in the quadrat was included and measured. Other grasses mentioned in the general introduction only occurred occasionally and hence were not considered for analysis.

Nearest-neighbour analysis (i.e. aboveground canopy diameters of any individual species of any pair versus distance between them) was employed for the detection of competition between pairs of individual grasses after verifying which species were relative dominants and co-dominants, both in canopy cover and number of individuals.

Counting of individuals was done for the determination of dispersion index (R). Clark and Evans (1954) used the dispersion index to determine the significance of departure from randomness towards both regularity and aggregation of populations or communities.

$R = \bar{r}_a / \bar{r}_e = (\Sigma r)(2\sqrt{\rho})/n$, where $\bar{r}_a$ is the mean observed nearest-neighbour distance (r/n), r = measured distance to the nearest-neighbour, n = number of such measurements and $\bar{r}_e$ = the expected mean nearest-neighbour distance given random

dispersion $(1/2\sqrt{\rho})$, where ρ = density and is expressed as number of individuals per unit area. For example, if there are 30 individuals occupying a $10m^2$ plot, their density per unit area is 30 individuals/$10m^2$, which equals 3 individuals per unit area. The density estimate was obtained from the quadrat results. Phillips and MacMahon (1981) reported that the advantage of such distance based measures of dispersion is that the scale of the pattern examined is not restricted to any particular quadrat size.

Table 4.1.1:

Example on how the dispersion indices (R) were calculated:

Md versus Md:

$R = \bar{r}_a / \bar{r}_e = (\Sigma r)(2\sqrt{\rho})/n$
$= (35.08)(2\sqrt{8.65})/111$
$= 1.8590$

Md = Merxmuellera disticha

where $\bar{r}_a$ = the mean observed nearest-neighbour distance (r/n), r = measured distance to the nearest-neighbour, n = number of such measurements and $\bar{r}_e$ = the expected mean nearest-neighbour distance given random dispersion $(1/2\sqrt{\rho})$, where ρ = density and is expressed as number of individuals per unit area. Units for nearest-neighbour distances are cm or m.

4.1.4: RESULTS

H. hirta, M. disticha and T. triandra each tend to occur in monocultures on both the east- and west-facing slopes. H. hirta tends to be dominant in terms of number of individuals per quadrat, and M. disticha dominates in terms of area cover per quadrat, whilst T. triandra has become moribund on both the slopes surveyed.
The results of the dispersion index (R), abundances, densities and dominance of the three species, are as tabulated in 4.1.2, 4.1.3, 4.1.4 & 4.1.5

The tabulated dispersion indices (R) revealed that five out of six pairs tested departed from randomness towards regularity, i.e. $R > 1$, whilst only one pair tended towards aggregation, $R < 1$. H. hirta dominated in both abundance and density, whilst M. disticha was most important only in relative dominance, in the 1975 burn (both of which occurred in the east- and west-facing sections of the gradient). In the 1988 burn M. disticha proved most dominant for both the standard measures of the three different grass species analysed; H. hirta was second and T. triandra was the least dominant of the three.

Graphically the species are associated as follows:

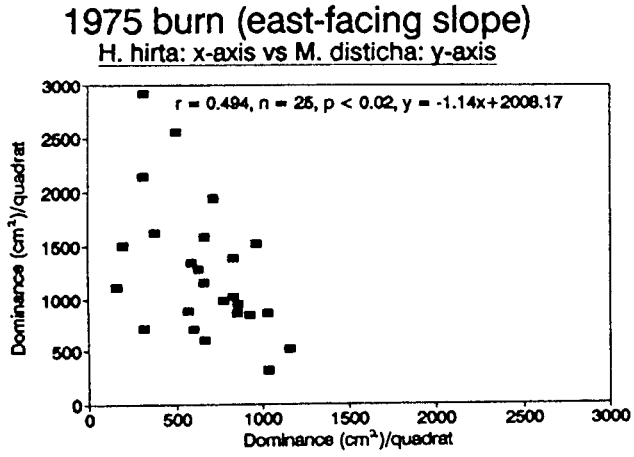


Fig.4.1.4a: Dominance-dominance regression for grass species named above.

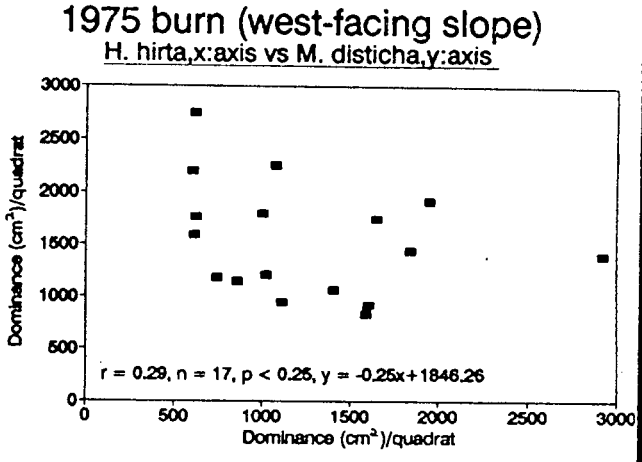


Fig.4.1.4b: Dominance-dominance regression for grass species named above.

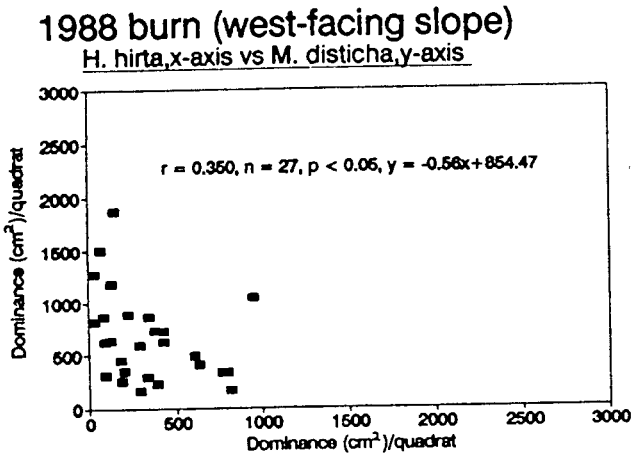


Fig.4.1.4c: Dominance-dominance regression for grass species named above.

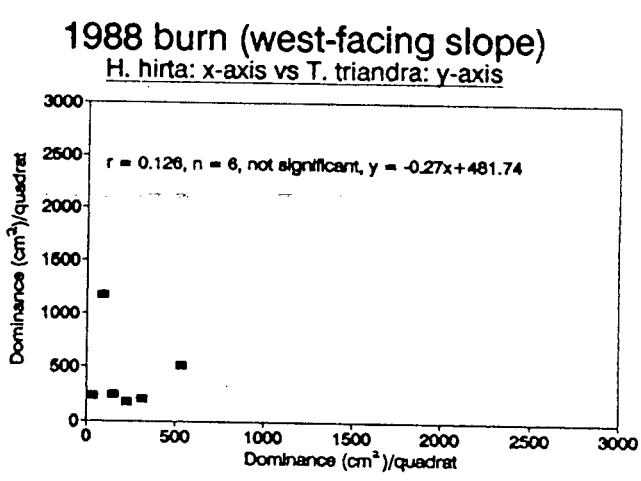


Fig.4.1.4d: Dominance-dominance regression for grass species named above.

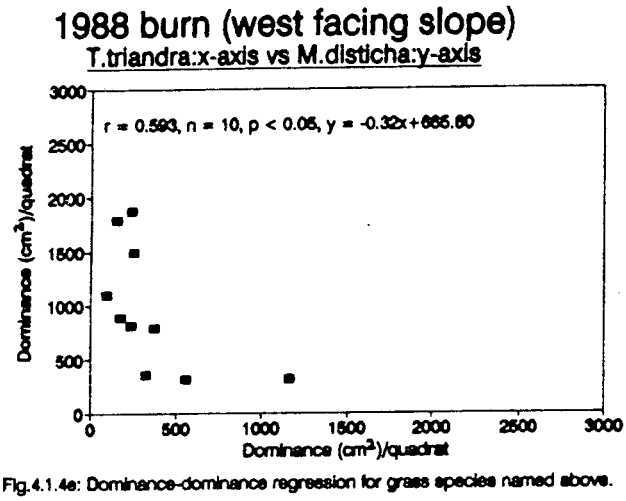


Fig.4.1.4e: Dominance-dominance regression for grass species named above.

Table 4.1.2: Dispersion index (R) for species pairs on Signal Hill's east- and west- facing slopes, (1975 burn), R < 1 = aggregated, R = 1 = random, and R > 1 = regular (i.e. specific value for regularity is, R = 2.1491, Clark & Evans 1954).
Key to species nomenclature: Hh = Hyparrhenia hirta, Md = Merxmuellera disticha and Tt = Themeda triandra; and n = number of pairs sampled.

Pair of species	n	site (slope)	dispersion index, R
Md vs Md	113	east-facing	1.2431
Md vs Hh	111	east-facing	1.8590
Hh vs Hh	113	east-facing	0.9734
Md vs Hh	107	west-facing	1.8903
Md vs Md	64	west-facing	1.6906
Hh vs Hh	66	west-facing	2.2630

Table 4.1.3: Distribution of grasses on the east-facing slope of Signal Hill (1975 burn). (number of quadrats, n = 34). Dominance is in m^2.

	H. hirta	M. disticha
Abundance	5.765	2.882
Dominance	0.080	0.156
Density	5.765	2.882
Relative density	66.7%	33.3%
Relative dominance	34.0%	66.0%

Table 4.1.4: Distribution of grasses on the west-facing slope of Signal Hill (1975 burn). The number of quadrats, n = 20 in this case, and dominance is in m^2.

	H. hirta	M. disticha
Abundance	7.65	2.85
Dominance	0.128	0.156
Density	7.65	2.85
Relative density	72.9%	27.1%
Relative dominance	42.2%	54.8%

Table 4.1.5: Distribution of grasses on the west-facing slope of Signal Hill (1988 burn), number of quadrats, n = 38, and dominance is in m^2.

	H. hirta	M. disticha	T. triandra
Abundance	4.281	4.588	3.120
Dominance	0.032	0.065	0.013
Density	3.605	4.105	2.053
Relative density	36.9%	42.0%	21.0%
Relative dominance	29.3%	59.2%	11.6%

4.1.5: DISCUSSION

The quadrat analysis indicates that H. hirta had the highest relative density both on the east- and west-facing slopes, whilst M. disticha was also common on both slopes but to a lesser degree than H. hirta on the east-facing slope (1975 fire burns), an antithesis to Ellis (1971), Teerie and Stowe (1976); and others referred under introduction-4.1.2 who expected great differences in mix between C_3/C_4 in cool temperate rainfall regions. The fact that both H. hirta and T. triandra occurred on both the slopes investigated, might suggest that they are generalists, or exceptions that occur both in tropical hot regions and cool temperate rainfall regions. Their conspicuous presence on parts of the cooler winter rainfall regions (e.g. Signal Hill) calls for extensive investigation, but a modest investigation of their biological behaviour might shed some light as to their distribution in a winter rainfall region.

Positions of the ridges are as referred under sections 4.1.3. (Materials and Methods). Nonetheless T. triandra occurred sporadically on both the slopes. This is attributed to unmanaged burning of the area. The fact that H. hirta was predominant in density, made it possible for it to peak in relative density whilst M. disticha's relatively profuse canopy cover allowed it to have the highest relative dominance.

On the west-facing slope on the veld which had burned in February 1988, M. disticha had the highest relative density and relative dominance, followed by H. hirta and lastly T. triandra. Sampling by quadrat method in conjunction with nearest-neighbour analysis indicated a significant departure of the sampled grasses from randomness towards regularity; only one of the six pairs tended in the direction of aggregation. Why 83.3% of the pairs sampled tended towards uniformity, and only 16.7% towards an aggregated pattern can be explained in terms of the increase in grass sizes. Several authors (Shreve 1942; Went 1955; Cooper 1961; Laessle 1965; Anderson, Malik and Jacobs 1969; Mâlik, Anderson and Myerscough 1976; Christensen 1977; Schlesinger and Gill 1978; Nakagosi et al. 1983; Herrera

1988; Chapin III et al. 1989) have found patterns tending towards regularity when plant size increases. In other words competition becomes more intense and more important as individuals grow larger. Small plants are eliminated from the high density phases of a mosaic, especially in homogeneous environments subject to intense stress (King and Woodell 1973). Thirteen to 14 years without disturbance is probably long enough to allow self-thinning and hence regularity of distribution. Regular pattern had been reported by several ecologists at different sites of varying environmental conditions of the world (Cottam 1955; Beals 1968; Wright 1970; Waisel 1971; Barbour et al. 1977b).

McDonough (1965) reported that mortality in an initially aggregated population of desert plants reduced the differences between high and low density patches, and resulted in a trend towards random dispersion of survivors; and that continuation of this process might be expected to produce a regular pattern as plants which occur closer than a critical distance to their neighbours thinned out. Analogous processes probably lead to regular patterns of grasses on Signal Hill. At a series of desert sites Walter (1962), and Woodell, Mooney and Hill (1969) asserted that regular dispersion in low rainfall areas and aggregation in higher rainfall areas were observable, suggesting that regular spacing may have been a result of competition for water. Yeaton and Cody (1976) and Smith (1979) have regarded larger distances between plants as evidence for competition for water. Other authors (Anderson 1967, 1971; Barbour 1973; Ebert and MacMaster 1981) have rebutted this belief. Ebert and MacMaster suggested that a sampling artifact might be responsible for such findings, i.e. the result of an inability to recognize individuals that are close together, whilst Anderson (1967, 1971) and Barbour (1973) argue that there is little support for regular pattern. They argued that only one most detailed and unequivocal piece of evidence of Woodell, Mooney and Hill (1969) for regular pattern is not convincing enough. Anderson (1970) suggested that regular pattern is rarely reached because of the effect of

microtopography. Regular spacing on Signal Hill in the current study is inferred to have resulted from competition for moisture. Moreover Cape Town receives little or no rain in summer; the mean annual rainfall of Signal Hill is approximately 500mm. Also the regularly spaced bigger individuals of the grasses observed on Signal Hill are possibly, robust competitors who may have, presumably under drought conditions, suppressed their neighbours. No conclusive determinant as to what is responsible for the statuses of the C_4 grasses of Signal Hill was obtained.

4.2.1: COMPETITION AMONG SIGNAL HILL GRASSES: CANOPY COVER VERSUS PLANT-TO-PLANT DISTANCE

Competition, though a widely discussed ecological topic (Braun-Blaunquet 1932; Weaver and Clements 1938; Friedman 1971; Harper 1977; Antonovics and Levin 1980; Fowler 1981, 1982, 1984, 1986; Fowler and Antonovics 1981; Tilman 1982; Nobel and Franco 1986; Underwood 1986; Law and Watkinson 1988; Tilman 1989) is still perhaps the most elusive and controversial subject in the field of ecology. Different ecologists have strongly disagreed on the prevalence and importance of competition between and within species (Connell 1975, 1980; Wiens 1977, 1984; Connor and Simberloff 1979, 1984a & b; Strong, Syzsk, and Simberloff 1979; Ebert and MacMaster 1981; Hendrickson 1981; Strong and Simberloff 1981; Roughgarden 1983; Strong 1983; Gilpin and Diamond 1984a & b). A variety of methodologies have been employed in trying to solve this riddle. Amongst the techniques employed is nearest-neighbour analysis where the sizes of the two members of a pair versus the distance between them is measured. It is this technique which is the subject of this chapter. Competition is defined as any direct or indirect negative impact of one plant on another (Harper 1977). Its role in nature remains controversial and thus far no consensus has been achieved. Welden and Slauson (1986) showed that disagreements arise from failure to separate the two aspects of competition, i.e. intensity and importance. They defined intensity of competition as the degree of strain (damage) competition induces in an organism's well-being; and the importance of competition to the relative degree to which competition contributes to the overall decrease in growth rate, metabolism, fecundity, survival or fitness of an organism below its optimal condition. In the present study the two aspects have been reviewed to effect a more clear-cut insight of the role of competition on populations/communities of the current study site. Intensity is estimated by the slope of the regression of sum of sizes versus nearest-neighbour distance, whilst importance is measured (deduced) from the correlation

coefficient (r) of the graph. Sum of sizes in the present study is a dependent variable whilst nearest-neighbour distance is independent.

According to Pielou (1960, 1962) competition between plants may manifest itself in two ways:

(i) the distance between any plant and its nearest-neighbour will be positively correlated with the sum of their sizes; and (ii) there may be a lower limit to the distance between any plant and its nearest-neighbour, or in other words, each successful plant may have around it its own "territory" within which no new colonizers can establish themselves. Generally speaking, it is believed that similar species compete more strongly than dissimilar species. Accordingly, less negative interaction should occur between species than within species. But among ecologists who have applied Pielou's (1960) nearest-neighbour analysis technique to prove the existence of competition between plants and other sessile animals, a polemic arose as to whether inter- or intra-specific competition is more powerful. Yeaton and Cody (1976), Yeaton et al (1977), Yeaton (1988-unpublished) argue that nearest-neighbour analysis techniques show predominantly that interspecific competition is weaker than intraspecific competition, whilst Fonteyn and Mahall (1978, 1981) found evidence for the converse.

Phillips and MacMahon (1981) have practically proved that the intenseness and importance of competition is both species-specific and also environmentally-orchestrated. They argue that if one of the regression lines were to lie completely above the other, then on average, plants of any given size could occur closer together when it is that combination of species, than when it is either of the other combination. Welden and Slauson (1986) and Welden et al. (1988) came up with a similar conclusion to that of Phillips and MacMahon (1981). But in their examples sum of sizes is on the independent axis (x) and distances between the members of the pair on the y-axis, whilst the inverse was the case with (Phillips and MacMahon 1981). Also (Welden and Slauson 1986 and Welden et al 1988) have in

general found no significant differences in the intensity of competition within and between species combinations.

Notwithstanding the above highlighted pros and cons about the strength and importance of competition in nature, Pielou's (1960) nearest-neighbour analysis technique in arid, semi-arid and mesic areas, remains an invaluable tool for investigating competition. Woodell, Mooney and Hill (1969), Anderson (1971) and others have applied this technique to examine spatial relations of the aboveground part of vegetation, where a positive correlation between interplant distance and plant size has been considered as evidence for competition. The suitability of this technique to measure competition has nevertheless been criticized by others, specifically in the way Pielou used it, e.g. " distance sampling-by taking the distance from a random individual to its nearest-neighbour will obscure any but very local effects and is not necessarily informative about competition" (Hill 1973). Meagher and Burdick (1980) have also mentioned that this method may produce erroneous results which may lead to assignment of statistical significance where none exists. They pointed out that there have been violations of chi-square test assumptions in nearest-neighbour frequency analysis, which they believe could cause major alterations in interpreting such analyses. In spite of the anxieties about this technique, it is still widely used in measurement of competitive interactions between living sessile organisms.

More recent studies have combined statistical analyses of pattern with experimental studies of negative interference between neighbouring individuals, including resources for which the individuals compete. Yeaton (1978), Simberloff (1979), Smith (1979), Nobel (1981), Phillips and MacMahon (1981), Nobel and Franco (1986) employed this technique in disclosing competition for water and mineral nutrients necessary for survivorship, fecundity, etc of living organisms. Most studies of this nature have been centered around desert ecosystems because of their simple physiognomic structure.

In this chapter nearest-neighbour analysis was used to detect competitive interactions between Hyparrhenia hirta,

Merxmuellera disticha and Themeda triandra in a grassland on Signal Hill.

It is predicted that if competitive intensity and importance of C_3 versus C_4 reflect grass distribution in the country, C_3 grasses should be competitively superior to C_4 grasses on cool moist protected sites.

The following questions were addressed in this section:

i) Does an analysis of nearest-neighbour show that there is competition between C_3 and C_4 grasses on both the slopes?
ii) For any given plant size, is the nearest-neighbour smaller for two plants of the same species, or for two of different species?
iii) Is intenseness and importance of competition more conspicuous within species than between species?
iv) Are species competitively equivalent, or do they behave differently across sites?

4.2.2: STUDY SITES

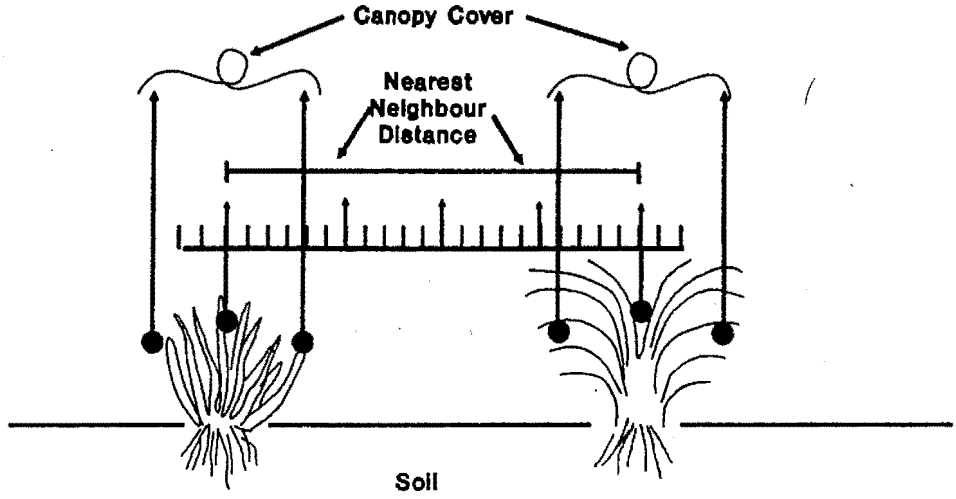
Detailed under section 1.3

4.2.3: MATERIALS AND METHODS

After verifying which species were relatively dominant and co-dominant, both in cover and number of individuals, nearest-neighbour analysis for comparing sum of sizes and plant-to-plant distances was employed to detect potential competitive interaction between pairs of individual grass species. Pairs of neighbouring species were randomly selected by throwing a stone in the air and choosing the nearest pair of individuals to where it landed. There was, therefore, neither qualitative nor quantitative preference of the grass canopy size in these measurements. The study areas are known to have been exposed to the same potential grazing and fire regime (1975 burn). This

minimized the effects of these disturbances on my sampling. Only data from live individuals were obtained for this analysis. Sampling continued until at least 40 pairs had been sampled for each analysis. This was done on both the slopes. Measurements of canopy covers and nearest-neighbour distances were done using a one meter ruler.

Fig.4.2.3 (a): Diagrammatical representation: canopy covers and nearest-neighbour distances measurements:



Hyparrhenia hirta Merxmuellera disticha

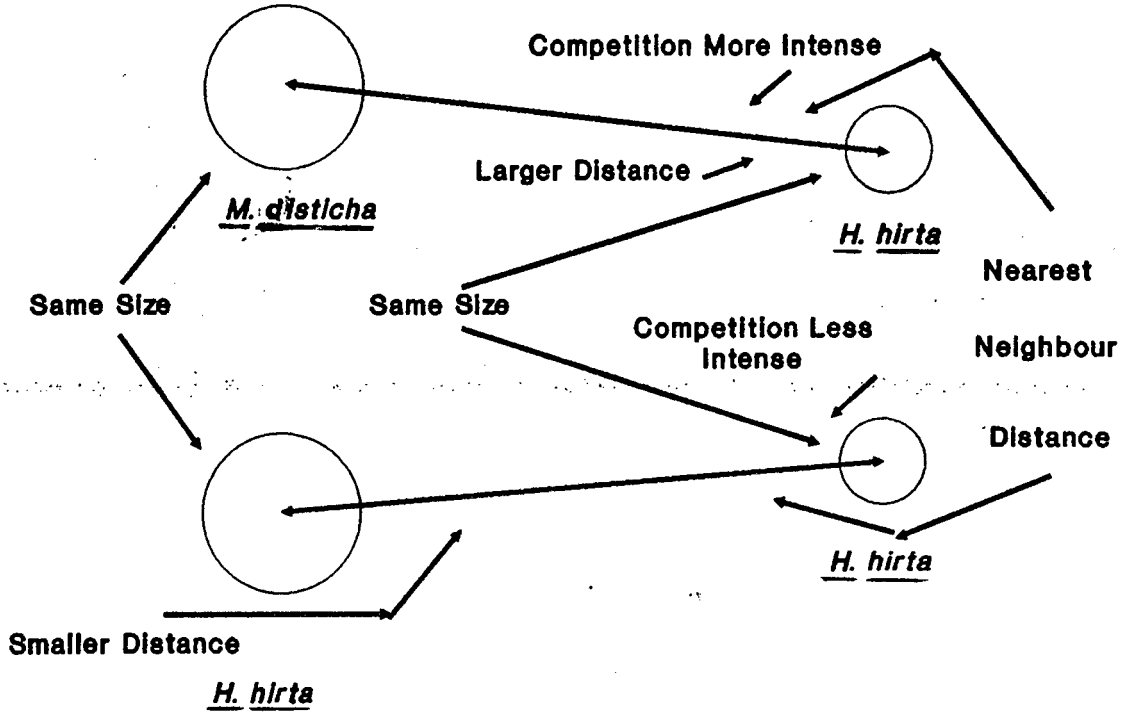
Similar methods were utilized on both the east- and west-facing slopes. The sum of the diameters of the individuals of any particular nearest-neighbour pair were regressed against plant-to-plant distances. Competition (or specifically negative interference) is considered to be occurring if a positive and statistically significant linear correlation is obtained (Pielou 1960, 1962). If the relationship is such that when the individual species are nearest-neighbours, their sizes are larger and when they are further apart their sizes became smaller, one would conclude that there is mutualistic interaction within and between living organisms.

The tolerance of one species for another was studied using a method in which the larger of the two individuals in a nearest-neighbour pair is regarded as determining the size of the other (Yeaton and Cody 1976). Thus the ratios of the

average of the sizes of the smaller individuals to the average of the distances from their neighbours were calculated for each pair of species. Each intraspecific pair was compared with the interspecific pair of which that species is the larger individual (Tables 4.2.4 and 4.2.5 on page 61).

A diagrammatical representation for species tolerance of one species for another is shown in fig.4.2.3 (b). Nearest-neighbour distances for diagrams on this page are distances after dividing standardized sizes (1m) of smaller individuals by the ratios of their (smaller individuals) sizes to the distances from their neighbours. The calculation of the ratios is defined on page 56.

Fig.4.2.3 (b): Diagrammatical representation: species tolerance of one species for another:



A larger distance between individual species implies less chance of coexistence, whilst a smaller distance between individual species implies high chance of coexistence.

Table 4.2.1: Calculation of ratios of the sizes of the smaller individuals to the distances from their neighbours.

Example: H. hirta versus H. hirta:

$$\text{ratio} = \frac{\text{mean of sum of diameters of smaller individuals of pairs}}{\text{mean of plant-to-plant distances of those pairs}}$$

$$= 15.1\text{cm}/22.9\text{cm}$$

$$= 0.66$$

The ratio is standardized by calculating it relative to a standard diameter of 1m for a smaller individual. Thus for the above example,

$$1\text{m}/0.66 = 1.52\text{m}.$$

Other distances were similarly calculated.

Statistical testing of these ratios was accomplished by applying a student's t-test to a logarithmic transformation of these values (Yeaton and Cody 1976, and Yeaton 1988-unpublished).

The slopes (gradients) and the correlation coefficients (r) of the pair of interacting species for both the east- and west-facing sites, on Signal Hill were respectively used to investigate the intenseness and importance of competition.

4.2.4: RESULTS

Among the three grass species analysed, all intra- and inter-specific nearest-neighbour pair were statistically significant, and positive linear correlation was found between the sum of nearest-neighbour canopy covers and their plant-to-plant distances (Tables 4.2.2 and 4.2.3):

Table 4.2.2: Regression (r) between nearest-neighbour distances and sum of their sizes on Signal Hill's east-facing slopes in vegetation last burned in 1975.
n = number of pairs of any particular species sampled,
y/x = slope of graph.

Pair of species	n	r	p	y/x	y-intercept
Md vs Hh	111	0.8659	< 0.001	1.26	4.94
Md vs Md	113	0.8283	< 0.001	1.47	10.14
Hh vs Hh	113	0.8300	< 0.001	1.06	9.57
Tt vs Tt	113	0.8360	< 0.001	1.31	10.67

Table 4.2.3: Correlations (r) between nearest-neighbour distances and sum of their sizes on Signal Hill's west-facing slope in vegetation last burned in 1975. n = number of pairs of any particular species sampled, y/x = slope of graph.

Pair of species	n	r	p	y/x	y-intercept
Md vs Hh	107	0.8927	< 0.001	0.92	15.46
Md vs Md	64	0.9279	< 0.001	1.36	1.73
Hh vs Hh	66	0.8492	< 0.001	1.02	7.73
Tt vs Tt	66	0.8194	< 0.001	1.12	12.37
Md vs Tt	71	0.7104	< 0.001	1.01	20.96
Hh vs Tt	41	0.6959	< 0.001	0.86	20.28

Key to species nomenclature for tables 4.2.2. and 4.2.3:

Hh = Hyparrhenia hirta
Md = Merxmuellera disticha
Tt = Themeda triandra

Results are also graphed (Figures 4.2.3a-j). Using distance measures, on both aspects there were in some cases significant differences in the tolerance of an individual for a member of its own species, or for a member of a second species that co-occurs with it. M. disticha (C_3) was a stronger competitor than H. hirta (C_4) on the east-facing slope (Table 4.2.4), whilst on the west-facing slope T. triandra was a stronger competitor than M. disticha (Table 4.2.5).

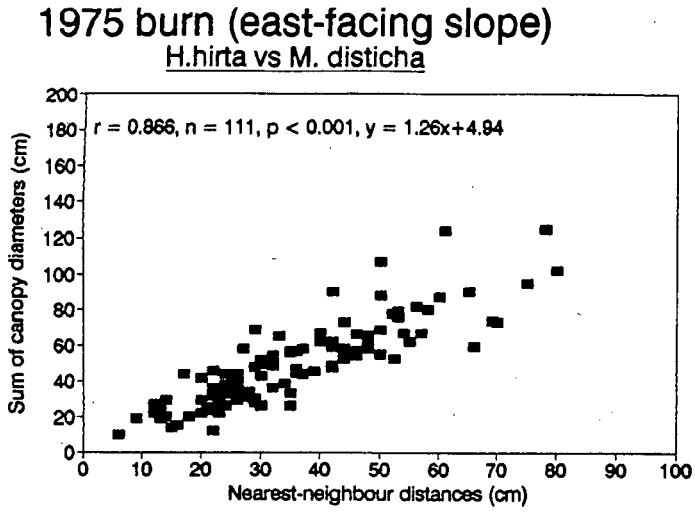


Fig.4.2.3a: Distance-size regression for grass species named above.

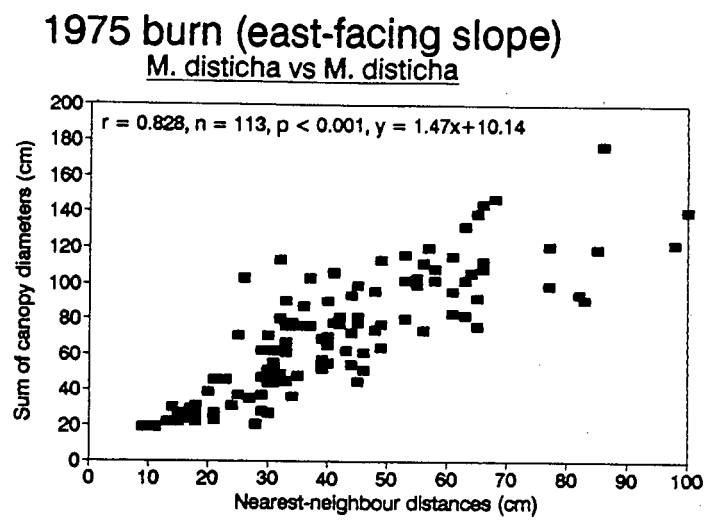


Fig.4.2.3b: Distance-size regression for grass species named above.

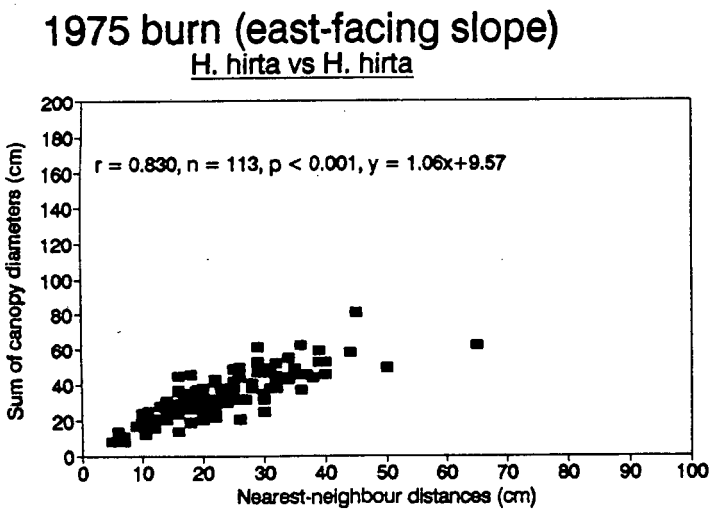


Fig.4.2.3c: Distance-size regression for grass species named above.

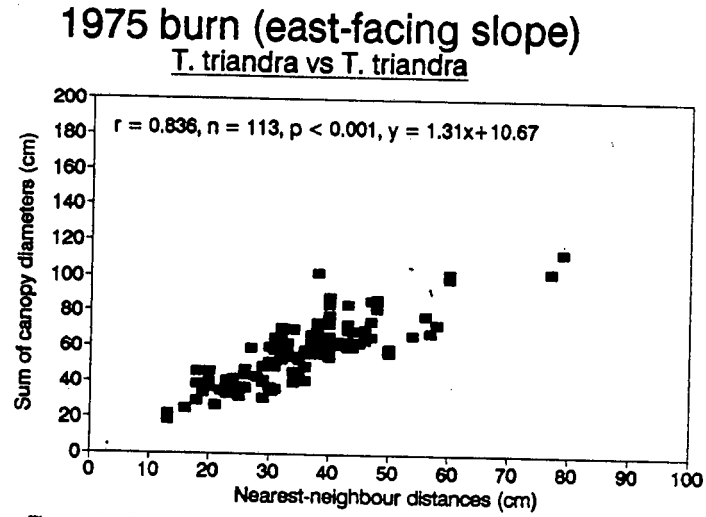


Fig.4.2.3d: Distance-size regression for grass species named above.

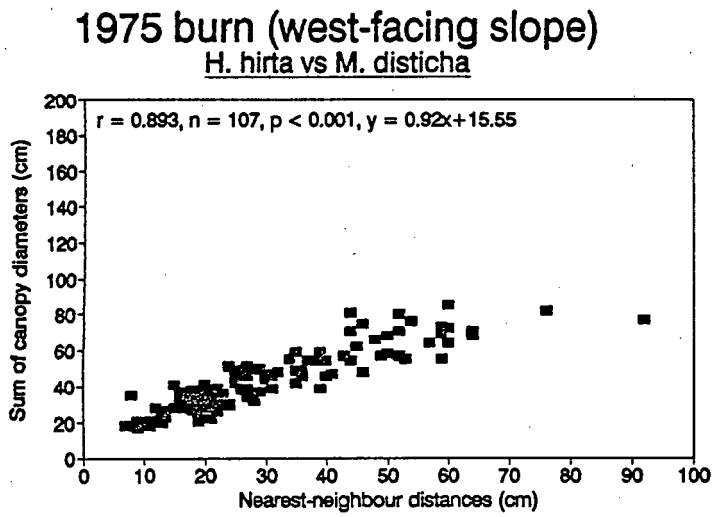


Fig.4.2.3e: Distance-size regression for grass species named above.

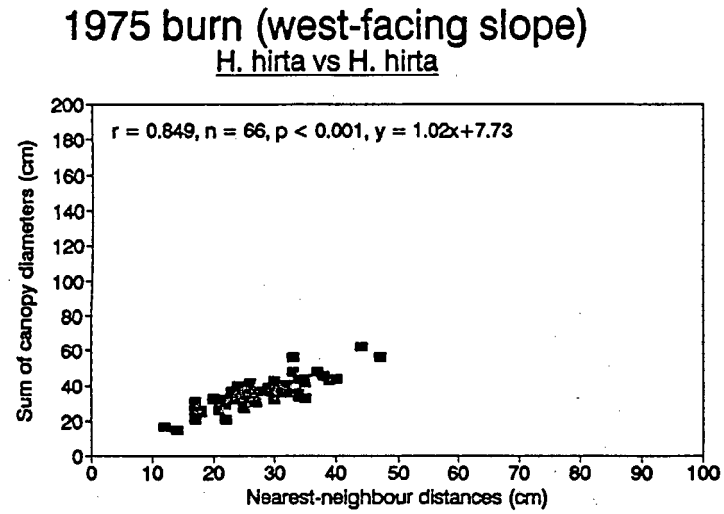


Fig.4.2.3g: Distance-size regression for grass species named above.

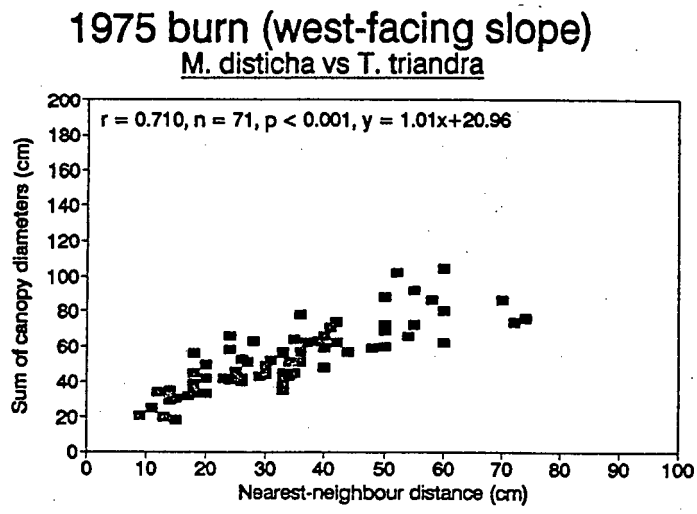


Fig.4.2.3i: Distance-size regression for grass species named above.

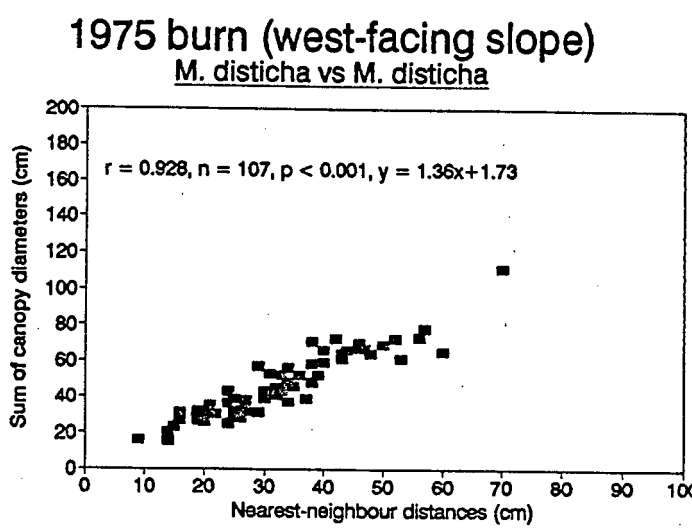


Fig.4.2.3f: Distance-size regression for grass species named above.

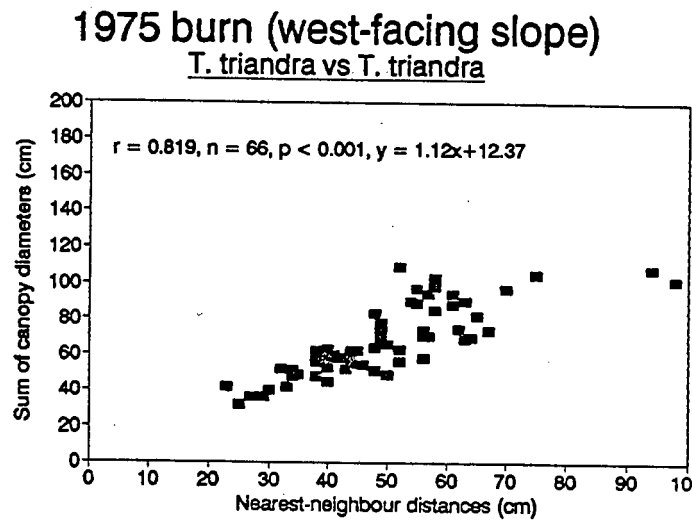


Fig.4.2.3h: Distance-size regression for grass species named above.

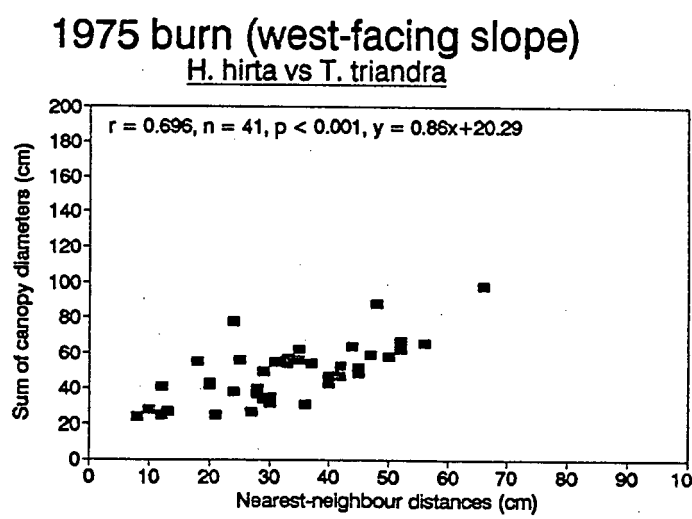


Fig.4.2.3j: Distance-size regression for grass species named above.

Tables 4.2.4 and 4.2.5: The average distance between nearest-neighbour pairs when the diameter of the smaller individual is fixed at 1m. * Larger individual is listed first, n.s.= non-significant, d.f.= degrees of freedom, inter = interspecific and intra = intraspecific, distances in the two tables are in meters (m), and ** = $p < 0.05$.

Key to species nomenclature:

Hh = Hyparrhenia hirta; Md = Merxmuellera disticha;
Tt = Themeda triandra.

Table 4.2.4: East-facing slope: 1975 burn.

*Intra	Mean distance	*Inter	Mean distance	t	d.f.	p
Md vs Md	1.41	Hh vs Md	1.63	0.853	119	n.s.
Hh vs Hh	1.52	Md vs Hh	2.13	6.143	201	0.05**

Table 4.2.5: West-facing slope: 1975 burn.

*Intra	Mean distance	*Inter	Mean distance	t	d.f.	p
Md vs Md	1.61	Hh vs Md	1.57	0.070	76	n.s.
Md vs Md	1.61	Tt vs Md	1.98	0.030	97	n.s.
Hh vs Hh	1.70	Md vs Hh	1.76	1.553	151	n.s.
Tt vs Tt	1.67	Md vs Tt	1.47	2.351	91	0.05**

In graphing of size-distance regressions, sum of canopy covers was a dependant variable (y-axis), and distance an independent one (x-axis), similar to Phillips and MacMahon (1981). The inverse was the case with Welden and Slauson (1986) and Welden et al. (1988). For further clarity see the two figures below:

The two figures below, from left to right, are from Phillips and MacMahon (1981), and Welden and Slauson (1986); they used the slopes of the figures below (graphs) to clarify intensity of competition between and within species.

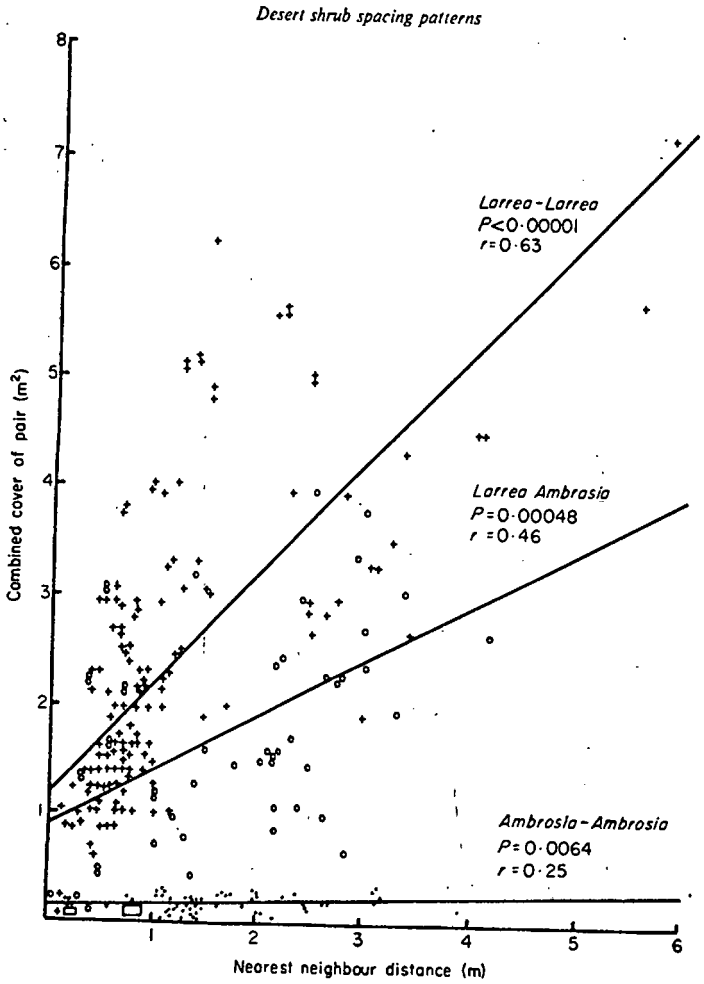


FIG. 2. Comparison of regression lines for *Larrea-Larrea*, *Larrea-Ambrosia*, and *Ambrosia-Ambrosia* nearest neighbour pairs at Organ Pipe Cactus National Monument, Arizona; *P* refers to the probability of obtaining by chance a value of *F* greater than that obtained in the regression analysis of variance. Symbols: + = *Larrea-Larrea*, ○ = *Larrea-Ambrosia*, • = *Ambrosia-Ambrosia*. The rectangles near the origin represent 20 *Ambrosia-Ambrosia* points.

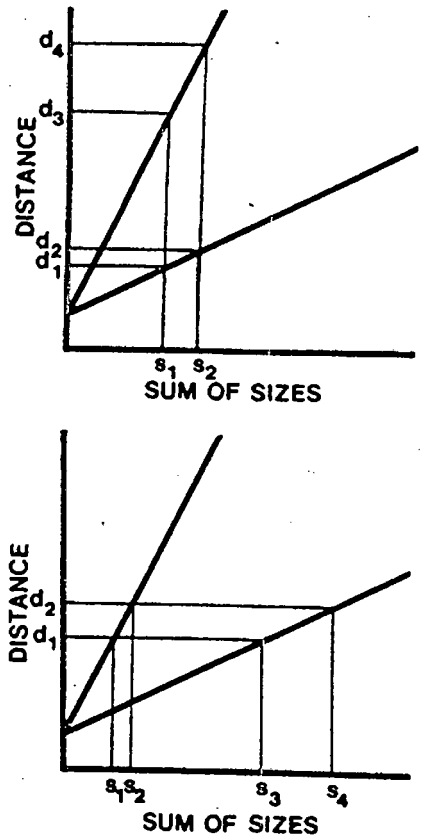


FIG. 2. TWO HYPOTHETICAL SIZE-DISTANCE REGRESSIONS, DIFFERING ONLY IN SLOPE

(A) The dependent variable is the distance separating a pair of plants, the independent variable is the sum of their sizes (e.g., canopy areas or basal areas). The steeper slope indicates more intense competition, because it associates a given increment in sum of sizes ($s_2 - s_1$) with a larger increase in distance ($d_4 - d_3 > d_2 - d_1$).

(B) The same hypothetical regressions. Again the steeper slope indicates more intense competition, because it associates a given increment in distance ($d_2 - d_1$) with a smaller increase in sum of sizes ($s_4 - s_3 > s_2 - s_1$).

4.2.5: DISCUSSION

The results of nearest-neighbour analysis on Cape Town's Signal Hill have disclosed that strong competitive interactions are occurring between all contiguous individuals both within and between species. The marked correlation between nearest-neighbour distance separating two grass plants, and the sum of their sizes, shows that the grasses in the community investigated are competing with each other for the available space. The marked disagreement between the results of the dispersion index ($R = 0.9734$, implies aggregation and a failure to reveal competition) and that of the correlation coefficients, ($r = 0.8300$, which indicated importance of competition), those for H. hirta versus H. hirta in the east-facing slope, suggest that some quadrats analysed for number of individuals were dominated by clumped seedlings or smaller individuals rather than by bigger adults. But the overall nearest-neighbour sampling on the east-facing slope was probably dominated by medium-, bigger-, and biggest-sized adults. Spatial heterogeneity in the environments, and restricted seed dispersal, have been reported to override the tendency for competition to produce regular distributions of plants, and positive correlations between plant sizes and distance apart (Phillips and MacMahon 1981). It has also been reported that measures of pattern are scale-dependent, and hence depend upon the choice of quadrat size and other sampling decisions (see Fowler 1986). It is, therefore, suggested that in the current experiment quadrat sizes have contributed to discrepancies in the results.

Though it is an inferential technique (Yeaton 1988-unpublished), nearest-neighbour analysis has been invoked by several ecologists as evidence for competition (Smith and Grant 1986; Herrera 1988). It was experimentally demonstrated that competition for soil moisture occurs within and between species (Fonteyn and Mahall 1978; Robberecht, Mahall and Nobel 1983; Ehleringer 1984 and Nobel and Franco 1986). The results of

nearest-neighbour analysis on Signal Hill were tested by experimental removals of neighbours, as detailed in chapter 5.

Though findings in this research might have been affected by other factors beyond the scope of this project, like anthropogenic disturbances, predators, diseases, herbivory, allelopathy, etc, significant positive correlations between cover and distance effectively showed that competition is playing a major role in structuring the grass community of Signal Hill.

The tolerance of an individual for a member of its own species, or for an individual of a second species, is rather complicated. In some cases individuals of different species are further apart than members of the same species, whilst in others similar species are further apart than members of different species. An example is one intra-inter-specific pairing (i.e. H. hirta versus H. hirta and M. disticha versus H. hirta, mean distances within and between members of pairs are 1.52m and 2.13m respectively- Table 4.2.4) in which interspecific distance is significantly larger than intraspecific distance. This suggests that M. disticha and H. hirta are less likely to coexist than M. disticha and M. disticha. Some intraspecific distances were, however, found to be significantly larger than interspecific distances (T. triandra versus itself and M. disticha against T. triandra- Table 4.2.5). This supports the observed distribution patterns of populations/communities on Signal Hill. It also appears reasonable to argue that both conspecifics and contraspecifics behave differently per patch in an area. For more on species tolerance see tables 4.2.4 and 4.2.5. In contrast, Yeaton and Cody (1976) and Yeaton et al. (1985) found that intraspecific competition is stronger than interspecific competition. However they argued that individuals of different species are equivalent ecologically if they maintain larger nearest-neighbour distances than similar-sized individuals of the same species. But Fonteyn and Mahall (1978, 1981), after a series of plant removal experiments, concluded that interspecific competition was usually stronger than intraspecific

competition. Findings at Signal Hill, Cape Town, where methods similar to those of Yeaton and Cody (1976), Fonteyn and Mahall (1978, 1981) & Yeaton *et al.* (1985) were employed, did not firmly establish which one is strongest.

On Signal Hill both inter- and intra-specific competition were in some instances statistically significant, whilst in others not. Nonetheless variations could be explained in terms of environmental differences such as changes in the soil texture, daily temperatures, etc. Statistically significant differences observed for Hh versus Hh (1.52m) compared to Md versus Hh (2.13m) - east (Table 4.2.4) and Tt vs Tt (1.67m) matched to Md vs Tt (1.47m) - west (Table 4.2.5), indicate that *M. disticha* is a threat to the long-term existence of *H. hirta* on the east-facing slope, whilst *T. triandra* is a stronger competitor relative to *M. disticha* on the west-facing slope. Regression slopes also indicate that on average competition is more intense between *M. disticha* versus *H. hirta*. The uncertainty about the conspicuous appearance of C_4 grasses in this region renders it risky to conclude that C_3 grasses are the long-term dominants in this current investigation. Nevertheless, considering the fact that there have been disturbances such as fire, grazing, etc in the past years, it might be reasonable to predict that C_3 grasses are in the long-term going to predominate if disturbances could be excluded. *M. disticha* is more likely to dominate on cooler east-facing slope than on the west-facing slope.

For other pairs of species there are also differences, though not in all. The smaller the regression slope, the larger is the distance between the members of a pair of that species (Tables 4.2.2 & 4.2.3). Significant differences for the slopes were unfortunately untested.

The intensity of competition between and within species was found to be relatively significant, and was both species-specific and site-dependent. This is because there had been some differences in slopes of the graphs between and within species on the two slopes sampled (Tables 4.2.2 & 4.2.3). However, intenseness and importance of competition were

conspicuous between species than within species (Table 4.2.2 & 4.2.3). This was attributed to the fact that the species are interacting with one another as if they are conspecifics rather than contraspecifics. Also it will be realized that the importance of competition on the east-facing slope was slightly more important in M. disticha versus H. hirta than between both M. disticha versus M. disticha, H. hirta versus H. hirta and T. triandra against T. triandra, whereas on the west-facing slope importance of competition between M. disticha versus M. disticha was found to be stronger than for the other five pairs (See Tables 4.2.2. and 4.2.3.). But since importance of competition is a long-term factor, it might be erroneous to conclude that M. disticha is the strongest competitor on both the slopes sampled. This is because reference to Table 4.2.5 reveals larger distances between T. triandra against M. disticha, than between M. disticha versus M. disticha, implying that T. triandra is more aggressive than M. disticha on the west-facing slope. This explanation does not ignore the fact that both intenseness and importance of competition are sometimes, if not always, site-controlled and species-specific.

The difference in correlations between and within species on the two different slopes, is ascribed to the fact that root system characteristics of the species are not always constant from one location to another. Singh (1964), Chew and Chew (1965), Barbour (1967), Garcia-Moya and Mckell (1970), Wallace and Romney (1972), Wallace, Bamberg and Cha (1974), Barbour et al. (1977a), Ludwig (1977) in Phillips and MacMahon (1981) reported different values of the root/shoot quotients depending on the locations. Spalding (1904), Cannon (1911), Barbour et al. (1977b), Yeaton, Travis and Gilinsky (1977) reported considerable variations in the vertical and lateral extent of roots in shrubs such as Larrea from place to place. Variations such as that are suggested on Signal Hill's east- and west-facing sections because of the differences between intra- and inter-specific competition. This is most likely when the limiting resource are extracted by the roots. Site of growth of any particular species and type of species itself should be

matters of crucial concern in ecological experimentation. This is because living organisms at any particular study area are most likely to develop lifestyles suitable for the areas of growth and development, or else they would be excluded. So differences in inter- and intra-specific competition in the east- and west-facing slopes are not very queer.

All in all intensity and importance of competition have been found significant on Signal Hill, and suggestions are that M. disticha will in the long-run outgrow the C_4 grass species on the east-facing slope, whilst T. triandra might dominate on the west-facing slope. M. disticha is not dominating because Signal Hill might have not yet reached competitive equilibrium. C_4 grasses are maintained, probably because of past disturbance regimes (see Chapter 3).

CHAPTER 5

5.0: USE OF REMOVAL EXPERIMENTS TO TEST FOR COMPETITION AMONG MATURE PLANTS

5.1: INTRODUCTION

Water is an indispensable resource throughout the organism's lifetime. Soil water potential is an all-important factor for plant germination, growth, survivorship, reproduction, etc. Competition for water has long been suspected between desert plants (Walter 1968; Cohen 1970). In mesic and arid environments, the effects of low soil water content can manifest themselves within a relatively short range of time. This can be displayed by members of the populations/communities, especially by weaker competitors losing their growth vigour, and ultimately dying out. Soil water availability was found to be a limiting factor for desert plants, e.g. in a bunchgrass, Hilaria rigida (Nobel 1980, 1981). However, other factors, such as diseases, could be limiting by causing death and infirmity in plants and animals.

Amongst the various techniques used to disclose competition for water and space amongst plant species, random removal of neighbouring individuals (one, or more than one species per individual) has been utilized (Sagar and Harper 1961; Putwain and Harper 1970; Fonteyn and Mahall 1981; Fowler 1981). The Scholander bomb (Scholander et al. 1965) proved to give good estimates of the xylem water potential of plant tissues (Boyer 1969; Wiebe et al. 1970), and hence it is now widely used to disclosing competition for water between plants.

Several removal experiments have revealed that when soil water availability is low, plant water status (leaf water potential) is affected by the presence of neighbours (Fonteyn and Mahall 1978, 1981). Removal experiments have demonstrated an increase in water potential around monitored plants on altered plots (Fonteyn and Mahall 1978, 1981; Robberecht, Mahall and Nobel 1983; Ehleringer 1984).

Improvement in plant growth, production, reproduction, longevity, etc following removals (Kincaid et al. 1959; Cable and Tschirley 1961; Cable 1969; Friedman and Orshan 1974, 1975; Parker 1985; Parker and Salzman 1985; Gurevitch 1986) have effectively demonstrated the occurrence of inter- and intra-plant competition for water. Leaf blades on monitored plants of altered plots remained green longer than those on monitored plants on unaltered plots (Nobel, Mahall and Robberecht 1983), and production was also greater on altered plots. The strong positive relationship between plant primary productivity and precipitation in warm deserts is clear evidence that water is a vital factor limiting production of both annuals and perennial shrubs (Walter 1968; MacMahon and Schimpf 1980; Ehleringer and Mooney 1983). Ehleringer (1984), through removal experiments, found that plants with neighbours excluded, had higher leaf water potentials, higher leaf conductances, and a greater leaf area than control plants. Growth rates and productivity output were found to improve dramatically for non-neighboured plants. Sharifi et al. (1983) found phenological patterns showing rapid growth rates in the spring and slower growth rates in the hot dry summer desert. They also found a positive association between low water potentials and reduced leaf sizes in summer.

It is the major goal of this current experiment to appraise the effect of removal of neighbouring plants on leaf (xylem) water potentials, longevities of both production and reproduction of the target individuals. An association of these results with competition might be unravelled. Prospects are that once individuals are secluded of neighbours, there might, or might not be an improvement in processes such as production and reproduction. In other words, roots of the remaining individuals might explore larger volumes of soil for water and nutrients.

5.2: STUDY SITE

Description of site of study is as in section 1.3

5.3: MATERIALS AND METHODS

(a) PLOTS SELECTION

Only plots which were virtually dominated by the two grasses, Hyparrhenia hirta (C_4) and Merxmuellera disticha (C_3) were used for this experiment. Themeda triandra (C_4), like the other grass species introduced in the general introduction, occurred marginally and was too rare for experimentation. Plot selection in the east-facing slope was limited to areas where nearest-neighbour analysis was carried out (on the 1975 burn), whilst on the west-facing slope, only a M. disticha monospecific patch (at the topmost point of the slope of the 1988 burn) was included in the two experimental design.

(b) APPARATUS AND SPECIES ANALYSED

Xylem/leaf water potentials were measured using a Scholander-type pressure chamber. There was an initial and final determination of an individual's leaf water potential. Initial leaf water potentials were measured before neighbouring individuals of some of the monitored species were removed. At least three weeks after removals, final measurements were determined. This was to ensure species adjustment and adaptability to the new, artificially induced environment.

At least twenty pairs (altered and unaltered individuals) of each species were monitored.

(c) REMOVALS AND MEASUREMENTS

Removal experiments were in two phases: The first one was pre-removal pressure bombing (measuring the xylem water potentials of all the individual species still neighboured): for H. hirta versus itself on the east-facing slope it was on the 21/02/1989, for H. hirta versus M. disticha on the east-facing slope it was on the 08/03/1989, for M. disticha versus itself on the west-facing slope it was on the 09/03/1989, for M. disticha versus H. hirta on the east-facing slope it was on the 27/09/1989, and for M. disticha versus itself on the east-facing slope it was on the 28/09/1989. Random removals of only one neighbour of some of the pressure bombed individuals were executed minutes after pre-removal pressure bombing in each case. Post-removal pressure bombings were conducted at least three weeks after initial pressure bombing. Post-removal pressure bombing dates are as follows: (species pairing sequence is as on pre-removal pressure bombings)- 15/03/1990, 13/09/1989, 23/03/1989, 13/03/1990, and 16/03/1990. This (post-removal pressure bombing) was carried out at least thrice over a period ranging from three weeks to six months, and it was found that the measured water potentials constantly varied. An average measure was therefore considered for statistical analysis.

The second phase was a removal of more than one neighbour around monitored plants. The experimental plants were in each case left with cleared circular plots of at least 1m around them, while control plants were not cleared of their neighbours. This second part of the experiment was done to assess growth, production, reproduction and leaf greening life span (see below for definitions). Six patches were chosen for this part: H. hirta, M. disticha, T. triandra monospecifics, and two mixed stands, one of H. hirta versus M. disticha and another one of H. hirta, M. disticha and T. triandra all on the east-facing section of the Hill. As with the first phase one M. disticha monospecific patch was monitored in the west-facing slope.

Dates of removals (in the east-facing slope) are for H. hirta versus itself - 15/02/1989, M. disticha versus itself - 15/02/1989, T. triandra versus itself - 14/02/1989, H. hirta versus M. disticha - 14/02/1989, H. hirta, M. disticha and T. triandra together - 09/02/1989; whilst M. disticha against itself on the west-facing slope was on the 08/02/1989.

All patches in the first phase measured about 10m x 10m, whilst in the second stage measured about 7m x 7m.

Counting of post-flowering tillers was done at least four months later, where necessary leaf greening longevity was monitored. Where possible counting of flowering tillers continued until early February 1990. Sizes of both neighboured and non-neighboured individuals were measured in other instances.

Growth as defined here simply refers to increase in the size of individual plants, whilst production refers to new leaves or culms produced by any particular plant, and reproduction implies post-removal flowering tillers produced by any individual plant, and leaf greening longevity refers to how long leaves of any particular plant persisted in their green colour before yellowing or desiccating.

(d) STATISTICAL ANALYSIS

Whether any significant difference in xylem water potential existed within and between species pre- and post-removal was tested using a Student t-test.

5.4: RESULTS

(a) XYLEM WATER POTENTIAL

Removal of putative competitors had, by inference from xylem water potentials, in some cases mildly affected soil water potentials. In other instances removal of neighbours had

substantially influenced xylem water potentials (see Table 5.1(a)). In other words less negative measurements were obtained where neighbour had been removed than in controls. A release from competition has in some instances resulted in a moderate soil water regime (inferred from xylem water potentials), whilst in other cases a most favourable soil water environment was created (also inferred from xylem water potentials).

(b) XYLEM WATER POTENTIAL: STATISTICAL ANALYSIS

See Table 5.1b:

(c) GROWTH, PRODUCTION, REPRODUCTION AND OUT-OF-SEASON LEAF GREENING

Remarkable changes in sizes of monitored plants of H. hirta and M. disticha on cleared plots were observed by the end of the growing period whilst such changes were not noticed for plants on uncleared controls. Generally, there was a positive relationship between plant size and number of their flowering tillers (see Figure 5 on page 77).

Production of new leaves and culms for H. hirta, M. disticha and T. triandra was substantial in the removed treatments whilst little or no change was observed for unaltered controls (data on this not shown). Out-of-season leaf greening was also observed in removal treatments but not for monitored ones on unaltered plots in all the three species studied. Significant differences in terms of number of flowering tillers between removal treatments and control plants of one batch of H. hirta was found (Wilcoxon test by ranks: $Z = 2.815$, $p < 0.005$, total observations = 22). The monitored individuals did not have flowering tillers at the start of the experiment.

Multiple range test for batches of H. hirta pairs revealed some differences in terms of competition. For example, individual species on some altered plots responded in the same way as those on unaltered plots (Tables 5.2 (a) and (b)).

Table 5.1 (a): Comparative results of field measured pre- and post-treatment xylem water potentials (in MPa) for H. hirta and M. disticha. Post-treatment xylem water potential was measured at least three weeks after initial readings.

Plot	Species pairs	Pre-treatment AVGS A^b Rmvl	Pre-treatment AVGS B^b Cntl	Pre-treatment STDS A^b	Pre-treatment STDS B^b	Post-treatment AVGS A^a Rmvl	Post-treatment AVGS B^a Cntl	Post-treatment STDS A^a	Post-treatment STDS B^a
A	Md vs Md	-2.9	-2.9	0.48	0.41	-3.0	-3.6	0.31	0.26
B	Md vs Md	-2.7	-2.9	0.39	0.43	-3.0	-3.4	0.33	0.26
C	Hh vs Hh	-2.3	-1.3	0.21	0.15	-2.2	-2.6	0.36	0.33
D	Hh vs Hh	-1.6	-1.7	0.38	0.32	-1.1	-1.6	0.24	0.27
E	Md vs Md	-2.5	-2.6	0.34	0.25	-1.2	-2.4	0.20	0.35

n = 30 for both controls and removals in plot A, in plot B, n = 18 for both controls and removals, in plot C, n = 20 for both controls and removals, in plot D, n = 22 for both controls and removals and in plot E, n = 31 for both removals and controls.

Key: Md = Merxmuellera disticha, Hh = Hyparrhenia hirta, species removed per individual (i.e. for group A only, group B individuals were not isolated of neighbours throughout the experimental period) are from plot A to E: Hh, Md, Hh, Md, Md. ^{b} = group of individual species pre-removal, ^{a} = group of individual species post-removal, Rmvl = removal, Cntl = control, AVGS = average measured xylem water potentials, STDS = standard deviations

Table 5.1 (b): Statistical analysis (a t-test) for the results of Table 5.1(a). @ = not significant, * = $p < 0.05$, ** = $p << 0.05$, d.f. = degrees of freedom.

Plot	Paired species	Removed species	Test statistic: A^b vs B^b Pre-treatment	p	Test statistic: A^a vs B^a Post-treatment	p	d.f.
							d.f.
A	Md vs Md	(Hh)	0.004	@	7.79	**	58
B	Md vs Md	(Md)	2.08	*	3.56	**	34
C	Hh vs Hh	(Hh)	0.44	@	3.68	**	38
D	Hh vs Hh	(Md)	1.38	@	6.42	**	42
E	(Md vs Md)[c]	(Md)	1.34	@	16.30	**	60

NB: All pairs (Tables 5.1a and b) but one, were sampled on the east-facing slope, the other (the very last pair in the table) was sampled on the west-facing slope. [c] = measurements were log-transformed (both pre- and post-treatments). Paired species, like for example, in Plot A (Md vs Md), means that two individuals of M. disticha were pressure bombed, and removed species, i.e. (Hh), in Plot A, means that one H. hirta next to one of the pressure bombed M. disticha was removed whilst the other M. disticha was left intact (i.e. still neighboured by H. hirta).

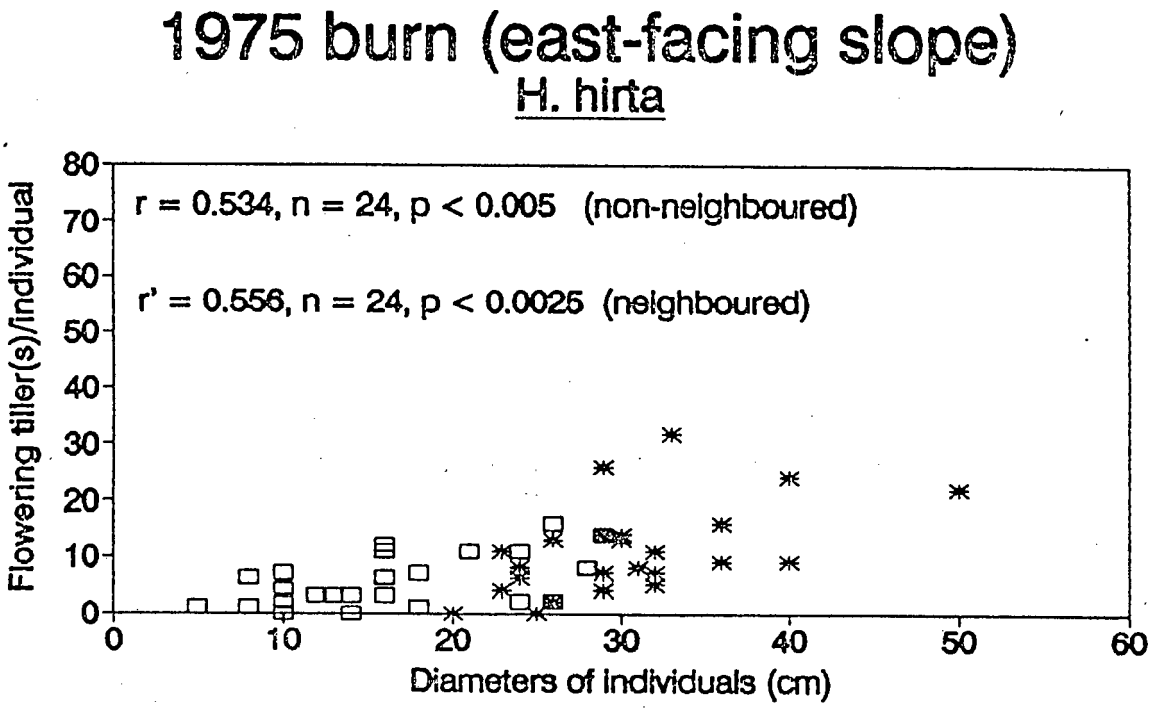


Fig.5: Size-number of flowering tillers regression for grass species named above.

* non-neighboured □ neighboured

Table 5.2 (a): One-way analysis of variance of flowering tillers for H. hirta.

F-ratio = 18.224, degrees of freedom = 191, $p < 0.0001$

Table 5.2 (b): Multiple range test analysis of flowering tillers for H. hirta.

Treatment	Group A	Group B	Group C	Count (n)	slope
1. Hh nonone		*	*	24	east-facing
2. Hh nei	*			24	"
3. Hh nonmore			*	50	"
4. Hh nei	*			50	"
5. Hh'nonmore''	*	*		22	"
6. Hh' nei	*			22	"

Key: Hh' = Hyparrhenia hirta- mixed stands (i.e. H. hirta with M. disticha).

Hh = Hyparrhenia hirta- monospecific.

nonone = non-neighboured individual with only one individual removed.

nei = neighboured individual

nonmore = non-neighboured individual with more than one individuals (sometimes two M. disticha and H. hirta, or three M. disticha and one or two H. hirta, and vice versa) removed.

nonmore'' = non-neighboured individual with two to four individuals of H. hirta removed.

* = under the same column implies non-significant difference between or among group of monitored individual species.

5.5: DISCUSSION

Removal of plants from pure stands of H. hirta and M. disticha, and mixed stands of H. hirta together with M. disticha, led to less negative soil water potentials as was observed by an increase in xylem water potentials of plants on altered plots. By inference there is therefore an increase, in soil moisture content and prolongation in the period of soil moisture availability for non-neighboured plant individuals. Removals also lead to changes in plant growth and reproduction. Both H. hirta, M. disticha and T. triandra responded to removals by an out-of-season leaf greening and new flowering tiller production. Neighboured controls of all the three species indicated no enhancement in these growth parameters, probably due to their unmodified water status. One pure stand of M. disticha showed significant pre-treatment difference in the xylem water potentials but these differences increased after removal treatments (Table 5.1 (b) - Plot B). This might indicate that individual neighbours removed were not strong competitors (if ever they were competitors), or the pairs might have been separated by optimal distances which effected no competition at all. Also soil moisture may have been at a critical stage so that both monitored non-neighboured and neighboured plants were not actively transpiring.

Large numbers of new leaves and culms produced by non-neighboured plants reflect a release from competition. The data showing the turnover of new leaves and culms were not analysed. There was nevertheless proportionality between new leaves produced and the sizes of the plants. Smaller plants also produced quite a large number of new culms. This might suggest that individuals have gained more from the exclusion of the potential neighbouring competitors. Soil nutrients such as nitrogen, phosphorus, potassium, etc that might have been left behind by removed plants might also have contributed to the observed improvement in leaf or culm production for non-neighboured individuals (both smaller and larger individuals). Nye and Tinker (1977) have reported on the importance of soil nutrients in the overall mechanism of competition.

Roots of five to six plants of each species on both cleared and uncleared plots were excavated. Some root extensions into new soil volumes were observed. This proves that water and space are some of the resources important for a plant's wellbeing.

The absence of predictable pattern between plant size and number of flowering tillers for control and removal treatments suggests that neighbouring competitors removed for the different individuals varied in their competitive effects. Thus a treatment plant which had a weak competitor neighbouring it benefited less from the removal of the neighbour or neighbours, than one which had a stronger competitor adjoining it. Inter-plant distances might be of importance in explaining variation in response to removal experiments. Similar-sized individuals separated from each other by bigger distances might compete less whilst individuals of their sizes separated by smaller distances might compete strongly. Sizes of neighbour(s) were positively related to their separation distances. This therefore calls for the need to consider both sizes and distances of neighbours before removing any potential competitor(s). Environmental parameters such as microhabitat heterogeneity (e.g. edaphic) might further confound any relationship between plant sizes and reproduction.

Multiple range test showed no significant difference in removal treatments (Table 5.2 (b)) (only one neighbour removed versus more than one neighbour removed). This suggests that competition by one and more than one of the removed individual species did not differ significantly before removals. Alternatively it might imply that soil moisture content was insufficient (not measured during that period) to encourage significant flowering on monitored altered plots. Insignificant improvement in flowering tillers or other reproduction parameters for monitored plants on unaltered plots were expected though. The fact that flowering tillers of H. hirta (on a stand of H. hirta with M. disticha) with one and more than one neighbour removed were statistically insignificantly different to those on unaltered plots, appear to prove that

sizes if not larger inter-plant distances of the removed individuals, or the combination thereof (sizes and inter-plant distances) were competitively ineffective.

The results of this study thus indicate intense competition since removal of neighbours lead to substantial increase in flowering, growth, productivity and changes in moisture status. Both inter- and intra-specific competition for water and space existed. There was, nevertheless, no significant difference in competition intenseness in terms of moisture status between and within species (Table 5.1 (b)). But for larger distances between plants, higher xylem water potentials were measured, whilst the converse was the case when distances were shorter between plants (Table 5.1(a)).

CHAPTER 6

6.0: EFFECT OF XYLEM WATER POTENTIAL ON CARBON UPTAKE AND PHOTOSYNTHETIC WATER USE EFFICIENCY

6.1: INTRODUCTION

The photosynthetic gas exchange characteristics of three grass species (outlined below) in the mediterranean climate region of South Africa (fynbos biome) were analysed. The objective was to investigate the effect of soil moisture content on carbon dioxide fixation rates of the two C_4 grass species, and one C_3 grass species occurring on Signal Hill, Cape Town. Removal experiments demonstrated an increase in xylem water potentials for individual grasses which were isolated of neighbours. Thus this experiment was aimed at disclosing whether an increase in xylem water potential implies an increase in carbon uptake.

Reports are that C_4 plants exhibit higher light-saturated photosynthetic rates, higher photosynthetic temperature optima, and higher photosynthetic water use efficiencies (WUE) than C_3 plants (Ehleringer and Bjorkman 1977; Ehleringer 1978; Vogel *et al.* 1978; Berry and Bjorkman 1980; Ellis *et al.* 1980; Pearcy *et al.* 1981; Pearcy and Ehleringer 1984; Robichaux and Pearcy 1984). *Hilaria rigida*, a C_4 desert grass, has the highest photosynthetic rate so far reported (Nobel 1980a).

This theory is applicable under certain specific environmental conditions. For example, C_3 plants perform well at temperatures of 15-25^{0}C whilst C_4 plants are favoured in the 25-38^{0}C temperature range. In a typical results, a C_4 grass, *Bouteloua gracilis* was found to have its net photosynthesis increasing at temperatures of 20, 30 and 40^{0}C, whilst the net photosynthesis of *Agropyron smithii*, a C_3 decreased (Kemp and Williams III 1980). A plant *Tidestromia oblongifolia* has been reported to optimally photosynthesize at temperatures of 46 and 50^{0}C (Bjorkman *et al.* 1972b). The optimum temperature for leaf photosynthesis was found to be

35^0C for a native C_4 grass, Trachypogon plumosus and an introduced African grass Melinis minutiflora (C_4), whilst for the other introduced African grass, Hyparrhenia rufa (C_4), it was 40^0C (Baruch et al. 1985). Ludlow and Wilson (1971) reported a mean of 38^0C for ten tropical grasses. Anomalies have nonetheless been reported where C_4 species can successfully compete in cool or shaded habitats (Pearcy and Troughton 1975; Caldwell et al. 1977).

A general belief amongst plant ecophysiologists is that the higher the xylem water potential, the greater is the rate of carbon dioxide fixation, and vice versa (Van der Heyden and Lewis 1989). Bazzaz and Carlson (1984), Zangerl and Bazzaz (1984) believed that carbon dioxide interacted with the availability of light and water. However, Van der Heyden and Lewis (1989) highlighted the scantiness of knowledge about photosynthetic carbon-gaining strategies of fynbos growth forms. It has also been shown that the rates of photosynthetic gas exchange of the evergreen sclerophyllous shrubs of the mediterranean climatic regions decline in most cases during the summer drought period (Mooney and Dunn 1970; Odening et al. 1974; Gigon 1979; Beyschlag et al. 1986).

A relationship between photosynthetic WUE and carbon dioxide fixation rate or photosynthesis (A) for the three grass species was investigated in the current chapter. Previous studies have shown a positive relationship between photosynthetic WUE and the surrounding carbon dioxide concentration (Strain 1987). Findings by other studies are for C_4 plant species possessing photosynthetic WUE of about 2-3.5 times that of C_3 plant species when compared under similar environmental conditions (Robichaux and Pearcy 1984; Slayter 1970; Ludlow and Wilson 1972; Bjorkman, Mooney and Ehleringer 1975; Ludlow 1976; Rawson, Begg and Woodward 1977; Brown and Simmons 1979; Osmond et al. 1980).

The experiments were done to test the assumption that changes in xylem water potential recorded in competition experiments also influence photosynthetic rates. Removal

experiments have indicated an increase in xylem water potentials for non-neighboured plants and not for neighboured plants. The three grass species growing in the cool, winter rainfall region of South Africa, on the east- and west-facing slopes of Cape Town's Signal Hill: Hyparrhenia hirta (C_4), Merxmuellera disticha (C_3) and Themeda triandra (C_4) were used for this experiment.

The following questions were asked:

(i) Is there any relationship between xylem water content and carbon dioxide fixation rates of C_3 and C_4 plants?
(ii) What is the rate of carbon dioxide fixation of a C_3 plant relative to that of a C_4 plant in the winter rainfall climates of Signal Hill?
(iii) Are there differences in photosynthetic WUE between and within species?

6.2: STUDY SITE

Detailed under section 1.3

6.3: MATERIALS AND METHODS

The three grass species (plantlets) utilized in this facet of the experiment are H. hirta (C_4), M. disticha (C_3) and T. triandra (C_4). At least nineteen juveniles of each of the three species were removed from Signal Hill (natural locations) and planted in pots. The soil into which seedlings were planted, was pre-watered. The plastic pots were some 170mm deep and 200mm in diameter.

Plants were excavated on a drizzly day to lessen adverse effects on plantlets parts through exposure. Each juvenile plant was dug with a large volume of protective soil completely covering all its roots. The planted individual species were then transferred to a greenhouse at the University of Cape

Town's Botany Department. They were kept there from February 07 to October 10, 1989. This was done to condition them to a greenhouse effect before their rates of photosynthesis were assessed. Plants were kept well-watered (up to three times weekly).

The first measurements of carbon dioxide fixation rates were carried out on October 03, 1989. The plants were under water stressed (droughted) treatments during that period. The two days chosen for experimentation were entirely clear, sunny and warm. Carbon dioxide fixation rate measurements were then performed in staggered fashion, i.e. if the first individual to be measured was Hyparrhenia hirta, the second would be M. disticha or T. triandra and thirdly T. triandra if not M. disticha. Before the second photosynthetic rate measurements were carried out on October 10, 1989, all individual potted plantlets were well watered. This was in the morning of the same day at about 07h00. Measurements of photosynthetic rates were then carried out between 11h30 and 13h30. During measurements (by enclosing a section of an attached leaf in a cuvette) each leaf utilized had its area estimated. On the second day of measurements (October 10, 1989) the same leaves used in the first day of measurements were utilized. In case a leaf utilized in the first day was damaged, a leaf positioned opposite it was considered a suitable surrogate. Area estimation was done by measuring the length and the width of any particular leaf portion enclosed by the cuvette. A field-transportable infra-red gas analyzer (IRGA) (LCA-2, Analytical Development Company Ltd., Hoddesdon, England) was used for the measurement of CO_2-assimilation rates (A), transpiration (E), stomatal conductance (Gc), stomatal resistance to water loss (Gr), water use efficiency (WUE), air and leaf temperatures. All data measured for these seven ecophysiological parameters were entered into a computer. Light intensity levels were maintained between 800 micromoles/m_2/s and 900 micromoles/m^2/s. Only 10 individuals of each species were considered for this part.

Xylem water potentials were measured using a pressure bomb (Scholander et al. 1965). This device has been shown to give good estimates of the xylem water potential of plant tissues (Boyer 1969, Wiebe et al. 1970). Measurements (xylem water potential) were carried out about ten to fifteen minutes after IRGA work. This time lag might influence the relationship between photosynthesis and tissue water potential recorded in this experiment. Air and leaf temperatures were quite high, and according to Kemp and Williams (1980), in favour of C_4 plants' photosynthetic optima during experimentation (See Table 6.1).

Photosynthetic water use efficiency was considered to assess the efficiency of water usage during photosynthesis between C_3 and C_4 plants and is expressed as net photosynthetic rate/transpiration rate (i.e. micromoles of carbon dioxide gained/mmoles of water transpired) at a particular xylem water potential.

Whether any significant difference in A and WUE existed within and between water stressed (dry) and water saturated (wet) species was tested using a two way analysis of variance (two way ANOVA).

6.4: RESULTS

(a) Gas exchange in relation to soil moisture content (soil moisture content was inferred from xylem water potentials).

The pattern of A for H. hirta, M. disticha and T. triandra under dry and wet conditions exhibited some differences (Table 5.1). Relatively lower photosynthetic rate values, were recorded for all species during the initial day of experimentation. The first day and second day average net assimilation rates (A) for both the three species are in table 6.1.

It was also found that in most cases photosynthesis was positively associated with xylem water potential (Table 6.1).

With some exceptions, a positive relationship between photosynthetic WUE and A for the ten individuals of each species existed both between and within species (Table 6.1- reflects averages thereof). In other words the relationship between photosynthetic WUE and A was not entirely conclusive because it was positive for some individuals but not for others. With few exceptions, WUE for C_4 grass individuals was almost twice that of C_3.

It was also interesting in some instances to notice quite strong correlation between stomatal conductance (Gc) and A in nearly all the three individual species analysed (Table 6.1- averages thereof). This was more pronounced in H. hirta where relatively higher values of A were obtained for relatively higher Gc values and vice versa (Table 6.1). A relatively smaller increase in A was attained for quite a bigger gap between initial and final Gc for a C_3, M. disticha compared to that of H. hirta (C_4) and T. triandra (C_4).

A two way ANOVA revealed statistically significant differences between initial and final photosynthetic rates and WUE between and within species (Table 6.2a & b). T. triandra (C_4) had both the highest assimilation rates and WUE and M. disticha (C_3) the lowest at both moisture levels (Table 6.1). There was no evidence that the C_3, M. disticha, responded differently from C_4 under different light intensities, temperature and moisture conditions.

Table 6.1: Results of comparison of averages of CO_2-assimilation rates (A), WUE, etc for the three grass species: H. hirta-C_4 (Hh), M. disticha-C_3 (Md) and T. triandra-C_4 (Tt) under droughted (dry) and undroughted (wet) conditions, 10 pairs of individuals were used for each species.

	Hh (C_4)		Tt (C_4)		Md (C_3)	
PRMT	AVG	STDS	AVG	STDS	AVG	STDS
PFDdry	841	0.010	855	0.013	861	0.012
PFDdry	863	0.013	862	0.014	867	0.011
ATdry	34.2	0.019	33.9	0.022	34.2	0.022
ATwet	32.3	0.044	35.0	0.023	34.6	0.036
LTdry	33.0	0.020	32.5	0.022	31.8	0.026
LTwet	33.8	0.017	31.9	0.026	29.5	0.051
XWPdry	-3.41	0.070	-3.23	0.172	-3.41	0.129
XWPwet	-1.03	0.144	-1.15	0.239	-1.49	0.147
Adry	7.97	1.227	13.69	4.487	6.48	2.551
Awet	12.61	1.429	23.85	3.433	9.21	3.176
Edry	7.42	0.106	9.76	0.125	14.07	0.255
Ewet	9.66	0.067	16.79	0.050	22.07	0.198
WUEdry	1.19	0.242	1.20	0.310	0.71	0.302
WUEwet	1.34	0.171	1.57	0.317	0.99	0.437
Gcdry	170.6	0.123	245.0	0.156	472.2	0.364
Gcdry	238.0	0.056	471.4	0.075	893.1	0.311

Key:
- PRMT = Parameter
- PFD = Photon flux density, or amount of light available for the plant and is measured in micromoles/m^2/s
- AT = Air temperature, measured in degree celsius (^{0}C)
- LT = Leaf temperature, measured in degree celsius (^{0}C)
- XWP = Xylem water potential in MPa (i.e. bars/10)
- A = Photosynthetic rate (A) in micromoles/m^2/s
- E = Transpiration rate, measured in mmoles/m^2/s
- WUE = Water use efficiency (micromoles of carbon gained/mmoles of water transpired
- Gc = Stomatal conductance, measured in moles/m^2/s
- AVG = Average
- STDS = Standard deviations

dry and wet, attached to each parameter refers to a condition under which a measurement was taken

Table 6.2a: Statistical analysis of photosynthetic rates (A) (log-transformed) and WUE of the three grass species, H. hirta (Hh), M. disticha (Md) and T. triandra (Tt) under saturated and stressed water conditions, 10 pairs of individuals were used for each species.

		A		WUE	
Source of variation	d.f.	F-ratio	p <	F-ratio	p <
Wet/Dry	1	41.038	0.0000	11.502	0.0013
spp	2	47.233	0.0000	16.797	0.0000
Interactions	2	1.031	0.3636	0.624	0.5396
Residual	54				

KEY: Wet = well-watered, Dry = water stressed, Interactions = Wet/Dry by species (spp).

Table 6.2b: Table of means of two-way ANOVA for A (log-transformed) and WUE for the three species of Table 6.2a.

	PHOTOSYNTHESIS (A)				WATER USE EFFICIENCY (WUE)			
	AVG		STND.ERROR		AVG		STND.ERROR	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
SP								
Hh	2.53	2.06	0.035	0.048	1.34	1.19	0.054	0.077
Tt	3.16	2.55	0.047	0.127	1.57	1.20	0.100	0.098
Md	2.16	1.80	0.121	0.112	0.99	0.71	0.138	0.095

KEY: Wet = well-watered, Dry = water stressed, AVG = average, SP = species, Hh = Hyparrhenia hirta, Tt = Themeda triandra, Md = Merxmuellera disticha

6.5: DISCUSSION

The results generally uphold the conventional wisdom that C_4 plants are photosynthetically advantaged under high temperatures (about 25 to 35^{0}C, sometimes up to 40^{0}C - Williams III 1974: and 46 to 50^{0}C in Tidestromia oblongifolia-Bjorkman et al. (1972b). However, without a cool temperature comparison it is difficult to confirm this. For all species analysed rather more negative xylem water potential (xwp) readings were recorded when the species were mildly depleted of moisture (dry), whilst higher (closer to zero) xwp values were found when species were well watered (wet). The results support a general notion amongst plant ecophysiologists that the higher the xwp, the greater is A. Since there was an increase in A following watering of the species, this suggests a positive relationship between soil water content, xylem water potential and photosynthesis.

Water potential of the three species were marginally different when water stressed. After hydration H. hirta showed a substantial change in its xylem water potential relative to the other two species. T. triandra also showed more marked change than M. disticha.

On average C_4 grasses had a relatively larger A than M. disticha (C_3). This is attributable to the relatively high air and leaf temperatures at the time of measurements which favour C_4 plant species (see Table 6.1). Factors other than temperature may be of significance in influencing photosynthetic capacity. Accordingly, when differences in the physical environment and life forms are taken into consideration, the photosynthetic capacities of C_3 and C_4 plants could be much more similar (Pearcy and Ehleringer 1984). The C_4 plants have been reported to assimilate carbon dioxide at higher rates than C_3 plants in hot climates (Berry and Bjorkman 1980; Pearcy et al. 1981; Pearcy and Ehleringer 1984), while at lower temperatures C_3 plants possess photosynthetic

rates as high or higher than those of C_4 plants (Pearcy et al. 1981; Dunn et al. 1987).

For all species a clear positive influence of soil water content, inferred from xwp, on photosynthetic rates was found (see Table 6.1). A greater increase in A for both H. hirta and T. triandra compared to that of M. disticha pre- and post-watering is ascribed to the fact that M. disticha generally indicated greater transpiration rate and lower photosynthetic water use efficiency (WUE). Consequently M. disticha lost quite a large amount of water, presumably in a short period of time. The result would be that it could not maintain its A for long if there were only a short-term water supply. Reinforcing this are observations both in the field and in the glasshouse. M. disticha had entirely closed their leaves to form closed cylinders once water supply was in deficit. This apparently resulted in its A being very low. On the other hand a closure mechanism might be of significance in keeping them alive perennially. It could therefore be concluded that M. disticha is more responsive to both hydration and dehydration relative to H. hirta and T. triandra. Nonetheless the two C_4 grass species have been observed to desiccate once there is a long-term stoppage of water supply. Generally C_4 grasses have shown a higher rate of photosynthesis following watering. T. triandra was found rather more favoured at both higher and lower water levels.

As reported under results, statistical analyses, have shown a significant difference between first day (droughted) and last day (watered) photosynthetic rates between and within species. The differences between initial and final photosynthetic rates within species indicate that A is possibly positively correlated with xwp, irrespective of whether a plant is C_3 or C_4.

The results of photosynthetic water use efficiency have indicated that C_4 grasses possess higher photosynthetic water use efficiencies than C_3 (M. disticha). Both C_4 grasses, H. hirta and T. triandra were shown to be statistically not different in their photosynthetic WUE. The difference that

existed between C_3 and C_4 plant species before and after watering was twofold. Differences in photosynthetic WUE have been reported for a wide variety of other C_3 and C_4 species. C_4 plants have been found to show photosynthetic WUE that are 2-3.5 times as high as those of C_3 species when compared under similar environmental conditions (Brown and Simmons 1979; Osmond et al. 1980; Pearcy and Ehleringer 1984). Current results, but on grasses under similar glasshouse conditions, have also indicated a similar 2-3.5 fold difference between C_3 and C_4 plant species, with C_4 plants showing higher photosynthetic WUE than C_3 species. Anomalies were encountered amongst individuals. Also inconsistencies in photosynthetic rates were observed. Such deviations within and between species might be assigned to artefact and experimental error, amongst other things. In the current study transplanting and planting of seedlings might account for some deviations from the normal trend. Other factors, such as age disparity, could also have contributed to discrepancies for both A and photosynthetic WUE.

The difference in photosynthetic WUE suggests a direct consequence of the difference in photosynthetic pathway between the two C_4 and a C_3 grass species. Robichaux and Pearcy (1984) have found C_4 Euphorbia species to exhibit high efficiencies of CO_2 utilization at low intercellular $p(CO_2)$, whilst C_3 Scaevola species exhibited relatively low efficiencies of CO_2 utilization at low intercellular $p(CO_2)$. Their argument was that C_4 Euphorbia species are able to keep higher rates of photosynthesis with lower leaf conductances (Gl) to CO_2 than the corresponding C_3 Scaevola species. A similar argument is suggested relevant to both C_4 species, H. hirta and T. triandra, and C_3 species M. disticha from Signal Hill. The fact that M. disticha was seen opening its leaves only when there was an increased water supply might be responsible for the low photosynthetic rate values and hence low WUE. M. disticha could possibly lose more water during the process of carbon dioxide intake, thus negatively affecting values of photosynthesis/transpiration (see Table 6.1- averages).

Pressure bombing has revealed that once their (M. disticha) leaves are closed, their xylem water potentials are very low, whilst at the same time C_4 grasses were still showing relatively high values.

It was presumed that there exists a positive interaction between soil water potential, xylem water potential, carbon dioxide fixation rate and WUE in all the species experimented under glasshouse conditions. It has been stated that under natural conditions (in the field) the effect of this large inherent difference between C_3 and C_4 species in their A and photosynthetic WUE may be modified significantly (Robichaux and Pearcy 1984) such that the differences usually present between C_3 and C_4 plants are greatly reduced.

There is a common assumption that plant species with high carbon fixation rates have the advantage of more available carbon for use in various ways (e.g. reproductive growth) and can compete favourably during the successional stages after a disturbance (Mooney et al. 1975; Solbrig and Orians 1977; Oechel and Mustapa 1979). Oechel and Mustapa (1979) found a strong correlation between plant cover and photosynthetic capacity across a geographical gradient of mediterranean scrub vegetation in southern California. This might imply that C_4 grass species analysed could cover larger area of Signal Hill than C_3 grass species during conditions that favour them (C_4 plants). This follows from their high carbon fixation rates than M. disticha (C_3) in the glasshouse.

Increases in xylem water potentials for plants in the glasshouse were higher (Table 6.1) than for plants on altered plots (non-neighboured plants) in the field. Soil moisture contents for both glasshouse and field plants were not measured. So it could not be confirmed whether a lesser increase in xylem water potentials for non-neighboured plants in the field relative to those plants in the greenhouse was due to low soil moisture content during experimentation (pressure bombing) days. It is thus suggested that removal of neighbours might cause an increase in xylem water potentials that is important photosynthetically.

CHAPTER 7

7.0: WHAT IS AN OPTIMAL SITE FOR SEEDLING ESTABLISHMENT?

7.1: INTRODUCTION

Reciprocal transplant experiments have long been used, amongst other techniques, to investigate the nature of limitations on the distribution and abundance of plants. Some areas are inaccessible to the organisms, whilst some are unsuitable for species of some genera and favourable for others. Species may impose limits to the distribution ranges of others by competition, predation, parasitism, etc, or alternatively some physical or chemical factors may be responsible. A large number of tropical plant species are commonly known not to be able to withstand low temperatures, with the frost line effectively restricting their distribution. Authors report a fine scale adaptation of plant species (Bradshaw 1984; Endler 1985, in Waser and Price 1985). In their reciprocal transplant experiments, Turkington and Harper (1979) found that clover genotypes grew best in their site of origin, and when competing in the greenhouse with the grass species that dominated the site. Transplant experiments have also been used to demonstrate local adaptation to abiotic rather than biotic conditions (Hickey and MacNeilly 1975; Davies and Snaydon 1976; Schemske 1984). Fowler and Antonovics (1981) found little evidence of local or regional adaptive differentiation, a phenomenon also reported by Waser and Price (1985)

On Signal Hill some Hyparrhenia hirta (C4), Merxmuellera disticha (C_3) and Themeda triandra (C_4) monospecific and mixed stands are evident. This chapter reports a reciprocal transplant investigation as to what could account for the observed grass distribution patterns and their proportions on Signal Hill. A growing awareness among plant biologists is that events occurring during the seedling stage of the life history of plants are the main causes of the distribution and abundance

of adults (Grubb 1977; Harper 1977; Hamrick 1979; Werner 1979; Gross and Werner 1982). Similar ideas have been expressed by Marks (1974), Platt (1975), Werner (1977), Rabinowitz (1978), Cook (1979).

To date there have been a number of studies done on reciprocal transplant-replant experiments, and seedling establishment experiments (Sagar and Harper 1961; Mark 1965; Cavers and Harper 1967; Miles 1972; Harper 1977; Turkington and Harper 1979; Van Meijden and Van der Waals-Kooi 1979; Gross 1980; Doust 1981; Goldberg and Werner 1983; de Hullu 1985; Werner 1985; Fowler 1986; Klinkhamer and De Jong 1988). Friedman (1971) conducted a study in the Negev Desert. Seedlings of the shrub Artemisia herba-alba were transplanted around the codominant shrub Zygophyllum dumosum. He found survival and growth of seedlings lower when they (seedlings) were planted next to the adult shrubs than when planted away from them.

This study was aimed at investigating the kind of relationship between transplanted seedlings of H. hirta and M. disticha into monoculture stands of their adults. With the aid of results of spatial pattern analysis, an attempt was made to identify the cause of grass patterns prevalent on Signal Hill's slopes. If species clumping reflects competitive interactions, better performance of seedlings should be found next to mature plants of conspecifics, than next to those of other species. On the other hand if short dispersal distance is the reason for clumping, seedling performance of the different species should not differ significantly closer to adults of different species. Also if the make-up of soil supporting the different stands is heterogeneous, seedlings of the two different species should differ in their performance on different stands. H. hirta seedlings should do well on monospecific patches of H. hirta when neighboured and non-neighboured, whilst the same should apply for M. disticha seedlings on M. disticha monocultures.

7.2: STUDY SITE

Plots of about 10m x 20m on the east- and west-facing slopes of Signal Hill were used for this investigation. Three patches on the east-facing slope, one monospecific for H. hirta and two monospecifics for M. disticha, all of the 1975 burn, and one M. disticha monospecific of the 1988 burn, were utilized for this purpose. The details of the overall study area are as in section 1.3.

7.3: MATERIALS AND METHODS

Seedlings were excavated from their prime location, which was at most 40m from plots to which seedlings were transplanted. Transplanting was carried out on a day with light drizzle to try to limit as much as possible any potential damage of the roots of the seedlings. In addition, seedlings were dug with their roots almost entirely protected by soil.

On transplanting, each seedling of H. hirta was paired with that of M. disticha in the following manner: in a monospecific stand of H. hirta, each H. hirta seedling was introduced at a distance of about 80mm from a H. hirta adult. Similarly the M. disticha seedling was planted in association with a different H. hirta individual. Non-neighboured seedlings of both H. hirta and M. disticha were each established at distances of about 350mm away from adults. A similar procedure was followed in a monospecific stand of M. disticha on both the east- and west-facing slopes. There were at least 12 replicates per plot on the east-facing slope, and at least 17 replicates per plot on the west-facing slope.

Seedling transplant dates were 28/02/1989 and 01/03/1989. Since drizzle during the following period was rather light and intermittent, artificial watering was provided. This was carried out on three occasions, on the 28/02/1989, 01/03/1989 and 03/03/1989.

Seedling sizes in terms of volumes (canopy diameters by heights) were measured a few months after transplanting, and again eight months thereafter. Neighboured and non-neighboured seedlings of both H. hirta and M. disticha were recorded for size (volume) gain or decrease. Means and standard errors of the log-transformed size differences of initial and final measurements were evaluated. Treatment effects as log-transformed size were tested with a two-way analysis of variance (Siegel 1956; Zar 1984). Two categories were established for group data: dead (missing or dried up); alive or producing new leaves.

7.4: RESULTS

Several seedlings died over the 13 months experimental period (see Table 7.1). There were significant differences between non-neighboured and neighboured individual seedlings, increasing or decreasing in aboveground volume over the experimental period. Non-neighboured grass juveniles grew much larger than neighboured ones (Table 7.2). In most cases seedling growth was greater closer to adults of their own species than that of the other (Table 7.2). M. disticha juveniles next to H. hirta adults decreased in sizes, whilst non-neighboured ones on monospecific stands have gained sizes (volumes) (Table 7.2). H. hirta next to conspecific adults have increased in volumes. Generally when adjacent to adults of M. disticha, H. hirta seedlings were disadvantaged (i.e. decreased in sizes) as were M. disticha seedlings next to H. hirta plants (Table 7.2). Decreasing in sizes (aboveground volumes) as referred here implies dying back of the seedling leaf area.

Through the use of a two-way ANOVA it was established that non-neighboured seedlings of H. hirta differed significantly from neighboured ones (Table 7.3a); neighboured individuals diminished in sizes whilst non-neighboured increased. There was no significant difference between juveniles of M. disticha neighboured and non-neighboured on M. disticha stands (Table

7.3a). For averages and standard errors of log-transformed volumes (sizes) of the seedlings see table 7.3b.

Table 7.1: The results of an experiment on the east- and west-facing slopes of Signal Hill for neighboured and non-neighboured seedlings of H. hirta (Hh) and M. disticha (Md) on monospecific stands of both H. hirta (Hh) and M. disticha (Md) adults. Data were recorded as dead or alive for both neighboured and non-neighboured seedlings. The plots were of two populations of M. disticha (n = 16 and 16 for neighboured and non-neighboured seedlings respectively) and (n = 12 and 16 for non-neighboured and neighboured seedlings respectively), and one population of H. hirta (n = 19 and 19 for neighboured and non-neighboured seedlings respectively) from the east-facing slope, and one population of M. disticha (n = 17 and 19 for neighboured and non-neighboured seedlings respectively) from the west-facing slope. Dead and alive refer respectively to number of seedlings which have died or lived during the 13 months of experimentation period.

	Seedlings					
	Neighboured		Nonneighboured			
	Hh	Md	Hh	Md	Adult population	slope
Dead	0	2	0	0	M. disticha	east
Alive	16	14	12	12	M. disticha	east
Dead	0	2	0	2	M. disticha	east
Alive	12	10	19	17	M. disticha	east
Dead	0	0	2	1	H. hirta	east
Alive	18	19	19	18	H. hirta	east
Dead	2	7	3	3	M. disticha	west
Alive	15	10	16	16	M. disticha	west

(Table 7.2): Results in terms of size (aboveground volume) decrease/increase of groups of H. hirta (Hh) and M. disticha (Md) seedlings with one group of each neighboured, and another group of each non-neighboured. The neighbouring adults are of M. disticha (Md) (three separate plots) and one plot of H. hirta (Hh). Average (AVG) volumes like individual volumes are measured in cm^3. Numbers 1, 2, 3 and 4 refer to the four experimental plots.

East-facing slope	Hh(seedlings)			Md(seedlings)		
	AVG	LN(AVG.DIFF)	STDS	AVG	LN(AVG.DIFF)	STDS
1. Md (adults)	-10	0.08	1.938	90	0.22	1.917
Md (no adults)	1011	0.83	0.892	109	0.29	0.584
2. Md (adults)	208	-0.48	1.722	78	-0.27	0.633
Md (no adults)	561	0.61	0.677	-179	-0.59	0.981
3. Hh (adults)	304	0.36	0.996	-47	-0.15	0.732
Hh (no adults)	717	0.77	1.024	170	0.03	0.778
West-facing slope						
4. Md (adults)	0.35	-0.12	0.898	75	0.88	1.942
Md (no adults)	473	0.53	0.714	75	-0.05	1.263

Key: (adults) = seedlings were neighboured by adults in that particular stand.

(no adults) = seedlings were not neighboured (by adults) in that particular stand.

AVG = average of sizes in terms of original (unconverted) aboveground volumes (sizes)

LN(AVG.DIFF) = average of differences between natural logarithms of measurements at the end and at the start of the experiment (aboveground volumes)

STDS = standard deviations thereof

East- and West-facing slopes = the two slopes where plots were sampled.

Table 7.3a: A two-way analysis of variance for differences of log transformed sizes (volumes), i.e. log(B)-log(A) of non-neighboured and neighboured H. hirta (Hh) and M. disticha (Md) seedlings of the three different monospecific stands of M. disticha (Md) and one monospecific stand of H. hirta (Md) as reflected in table 7.2 above. Letters B and A in brackets represent measurements at the end and the start of the experiments respectively.

Source of variation	Hh (seedlings) d.f.	F-ratio	p <	Md (seedlings) d.f.	F-ratio	p <
Removals	1	12.300	0.0006	1	0.823	0.3761
Areas (plots)	3	1.020	0.3865	3	2.393	0.0725
Interactions	3	0.543	0.6537	3	1.257	0.2929
Residual	117			108		

KEY: Interactions = Removals (neighboured and nonneighboured species) by plots

Table 7.3b: Table of means for log-transformed (Table 7.3a) sizes of aboveground volumes (in cm^3) of non-neighboured and neighboured H. hirta (Hh) and M. disticha (Md) seedlings of three different stands of M. disticha and one stand of H. hirta (Table 7.2 above). Only live pairs were considered for this analysis.

	Counts of seedlings: Nei & Non				Hh (seedlings) AVG		Hh (seedlings) STND.ERROR		Md (seedlings) AVG		Md (seedlings) STDN.ERROR	
P	Hh		Md		Nei	Non	Nei	Non	Nei	Non	Nei	Non
*	__	**	__	**								
1	16	12	14	12	-0.04	0.36	0.210	0.112	0.09	0.13	0.222	0.073
2	12	19	10	17	-0.21	0.26	0.216	0.067	-0.11	-0.25	0.086	0.100
3	18	17	19	18	0.16	0.33	0.105	0.108	-0.06	0.01	0.073	0.080
4	15	16	10	16	-0.05	0.23	0.102	0.078	0.38	-0.02	0.266	0.173

KEY: AVG = average(s), STND.ERROR = standard error, Nei = neighboured, Non = non-neighboured, P = plots, * = column of plots (areas), __ = columns of replicates of neighboured seedlings, ** = columns of replicates of non-neighboured seedlings.

7.5: DISCUSSION

The experimental results from seedling establishment experiments of both H. hirta and M. disticha demonstrated a negative interaction through nearest-neighbour analysis experiments between adults and seedlings of the different species. Non-neighboured seedlings generally increased in volume over the experimental period. This therefore suggests the necessity for open space and hence enough light, water and nutrients for seedling growth and establishment. Naturally occurring seedlings had a high death rate and few emerged under adult canopies of their own species (Friedman and Orshan 1975). Many removal experiment studies (Parker and Martin 1952; Glendening and Paulsen 1955; Cable and Tschirley 1961; Parker 1982, 1985; Parker and Salzman 1985) have reported an improvement in survivorship of non-neighboured grass seedlings. Soriano and Sala (1986) found that survival rates of transplanted seedlings of the grass Bromus setifolius increased away from shrubs. Density has also been reported to affect seedling survivorship (Schellner, Solbrig and Newell 1982). The fact that seedlings farthest away from adults improved their size status, suggests that soil water, nutrients and light might have been limiting closer to the adults. This might also indicate that adults of H. hirta and M. disticha could coexist as long as they are separated by larger distances.

Notwithstanding this observation of seedlings performing better when non-neighboured, there were exceptions. Non-neighboured M. disticha, in pure stands of M. disticha adults, generally deteriorated in terms of sizes. This suggests a preference for them to establish closer to their own parents rather than farther away from them. This interpretation is reinforced by observations of M. disticha seedlings having improved in sizes adjacent to adults of their own species in all stands sampled. Positive association was also found between juveniles of H. hirta and their conspecific adults. It appears therefore plausible that both H. hirta and M. disticha seedlings are positively associated with their own parents. It

is possible that once H. hirta and M. disticha are at a certain seedling phase, they recognize a "safe site" closer to their own parents for growth and development. A "favourable, or safe microsite" is defined as one in which seedling growth and establishment can occur (Harper et al. 1961 and Fowler 1988).

Both the seedlings of the two species in pure stands of contraspecific adults were generally negatively affected when closer to the adults, which might imply that individuals of one species (H. hirta seedlings close to M. disticha adults, and vice versa) do not prefer to grow closer to individuals of another species.

Seedlings growing next to their parents have been reported to enjoy protection from predation; with their rates of survival declining when the adults were removed (Parker 1982). McAuliffe (1986) found seedlings of the small tree Cercidium microphyllum suffering less herbivory-caused mortality under other perennials than in the open.

Through reciprocal transplants, clones of Trifolium repens were found to be locally specialized within a single field of permanent grassland, and specialization was inferred to be associated with the ability of specific clones to grow with specific grass species in the field (Turkington and Harper 1979). The fact that the intensity of suppression experienced by H. hirta seedlings from M. disticha stands varied from one stand to the other, could be explained in terms of the sizes of M. disticha adults that neighboured them. Possibly the bigger the adult neighbour, the more intense is suppression imposed upon an individual neighboured seedling. Similarly the extent of growth attained by each of the established neighboured seedlings of M. disticha on M. disticha stands could have been determined by the sizes of their neighbouring adults. Sizes of neighbouring adults were unfortunately not quantified in this analysis. However, sizes of neighbouring adults presumably played an influential role in determining the sizes of the introduced seedlings.

The fact that some of the established seedlings died, suggests that they (dead ones) might have suffered transplant

shock. Cavers and Harper (1967) found transplanted plants of Rumex crispus suffering transplant shock in an alien environment. Another possible factor responsible for transplanted seedling mortality could be the sizes of seedlings during time of establishment. The sizes of transplanted seedlings were not significantly different during establishment but might have experienced interactions by adults of varying sizes differently.

An instance where H. hirta seedlings improved their sizes when neighboured by M. disticha adults (Table 7.2) could be explained in terms of the adults neighbouring them. In other words, if the adults that neighboured them were relatively smaller, the stress of competition they would impose might be less or insignificant. However, the reasons for release from competitive inhibition are unknown in this instance. Non-neighboured M. disticha seedlings which decreased in sizes in the M. disticha monospecific stand might have suffered a transplant shock. It is possible that for edaphic or other microenvironmental reasons, safe sites were closer to their parents on that particular patch.

In conclusion, the results of this experiment suggest that familial clumping and competition, amongst other phenomena, have played a major part in patterning Signal Hill's grass community.

CHAPTER 8

8.0: EFFECT OF FIRE ON FLOWERING

8.1: INTRODUCTION

Veld burning has unquestionably been a feature of the African landscape since time immemorial. Periodic or planned burning of the veld is thought to preserve pasture grass communities (Scott 1970). The beneficial effect of veld burning may be merely the removal of excess cover, since where the veld has been grazed short or excess grass had been removed by mowing, there was no need to burn (Scott 1951). Many studies in various parts of southern Africa, such as the eastern Cape, Natal, and the north-eastern Transvaal have confirmed the necessity for regular/frequent fires for the maintenance of grassland communities (Acocks 1966; Rethman and Booysen 1968b; Tainton, Booysen and Scott 1970; Downing 1974; Trollope 1974; Trollope and Potgieter 1985; Friedel and Blackmore 1988). But there are studies who have reported the persistence of grasses on unburned treatment (Bowman, Wilson and Hooper 1988).

In general, however, fire appears a key factor in maintaining South African grasslands. The role of fire in preventing bush encroachment has also been demonstrated (Trollope 1974). To date many studies on fire have shown it to be the most important agent for improving grassland ecosystems. Grass species richness improved when burnt annually, and decreased when veld was protected from fire for at least five years (Yeaton *et al.* 1988). Season of veld burning might also play an important part in maintaining South African grasslands. Rethman and Booysen (1968b) found that production of *Themeda triandra* and its regrowth potential were significantly influenced by the season of defoliation. On their study (Opperman and Roberts 1978) of *Themeda triandra*, *Elyonurus argenteus* and *Heteropogon contortus* suggested an optimum disturbance (burning, grazing, cutting, or drought) time to

prevent damage to the shoot apices because that may have a detrimental effect on leaf, shoot and seed production.

System processes such as nutrient recycling and water relations have been proved to be fire dependent (Raison 1979; Van Wilgen and Le Maitre 1981; Stock and Lewis 1986).

It was the aim of this part of the study to compare the effect on growth and flowering of Hyparrhenia hirta (C_4), Merxmuellera disticha (C_3) and Themeda triandra (C_4) 9 months, 21 months and 15 years after burning on Cape Town's Signal Hill.

8.2: STUDY SITE

See section 1.3

8.3: MATERIALS AND METHODS

A survey of fire effects was carried out after a wildfire which burned an area approximately 50m x 150m of the topmost section of Signal Hill's west-facing slope. The fire burned in late February 1988 (Clive May - Kloofnek station supervisor - personal communication). Other plots on the east-facing slope studied here are all known to have had their last fire in 1975.

As reported in Chapter 1, the Signal Hill plant communities comprise grasses, shrubs and herbs, but only the localized patches dominated by grass (H. hirta, M. disticha and T. triandra) were the focus for this study.

The role of fire in the 1988 burn was assessed by counting the number of flowering tillers 11 months (on January 1989) after fire, and another count of the same individuals was performed on December 1989 and January/February 1990. Two plots, a monospecific stand of M. disticha, and a mixed stand of H. hirta and T. triandra were used. At least 20 individuals were monitored. Wire rods with numbered tags were used to mark the individuals monitored. It was not possible to compare M.

disticha versus itself between the 1988 burn and the 1975 one, because M. disticha on the 1975 burn failed to produce any flowering tillers. Flowering tillers were also counted on H. hirta and T. triandra in the 1988 burn. Growth in terms of individual species' sizes and leaf greening were slightly observed for both the 1975 and 1988 burn. The data thereof was not analysed.

Xylem water potential measurements of the three grass species on two unaltered plots in the 1975 burn (east-facing slope) were done on the following two days: 05/10/1988) and 21/02/1989. The aim was to use the measurements to explain the differences in the vigour of growth and reproduction of the three grass species.

8.4: RESULTS

Flowering in M. disticha was more strongly stimulated by fire in the summer of 1988/1989 than that of 1989/1990 (Wilcoxon test by ranks: $Z = 3.214$, $p < 0.005$, total pairs = 25). Flowering tillers produced between nine and 11 months after fire were significantly more abundant than those produced 21 to 24 months thereafter (see Figures 8.1 & 8.2 on page 109).

H. hirta and T. triandra species on a 1988 burn showed leaf greening and flowering longer than those on the 1975 burn. Growth in terms of size of individuals were considered insignificant for analysis.

Neighboured H. hirta on a 1975 burn showed, to a certain degree, an out-of-season growth, production and reproduction, whilst M. disticha and T. triandra on the same plots did not. The xylem water potential of H. hirta (-10.9(±0.29)), M. disticha (-14.6(±0.80)) and T. triandra (-13.8(±0.29)) on one stand differed significantly from one another other ($p < 0.0001$), and that of H. hirta (-19.7(±0.81)) and M. disticha (-34.5(±1.26)) on the other stand also differed significantly from each other ($p << 0.0001$). One way ANOVA thereof (1975 burn) produced the following (F-ratio = 13.893; degrees of

freedom = 29, $p < 0.0001$), and for H. hirta versus M. disticha, (F-ratio = 97.605; degrees of freedom = 23, $p << 0.0001$). Multiple range analysis test revealed a significant difference between xylem water potentials of H. hirta from that of M. disticha and T. triandra but not between M. disticha and T. triandra.

Normal annual flowering for H. hirta (C_4), and T. triandra (C_4) (to a lesser degree relative to that of H. hirta) was observed in the 1975 burn. There was insignificant or no flowering for M. disticha (C_3) in the same aged veld.

February 1988 burn (westward slope)

M. disticha

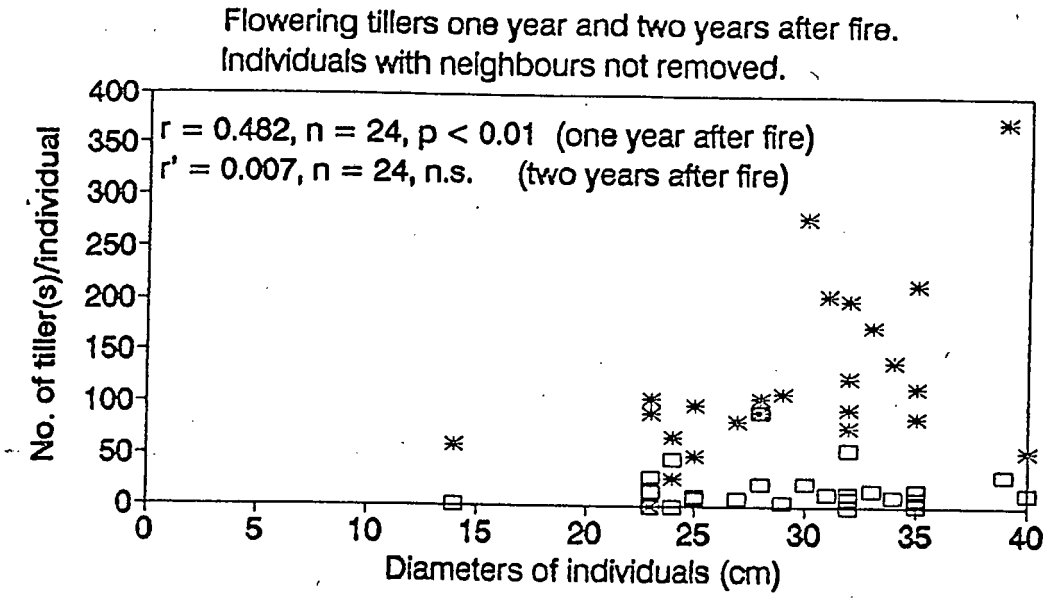


Fig.8.1: Size-number of flowering tillers regression for grass species named above.

* Tillers 1yr after. □ Tillers 2yrs after.

February 1988 burn(westward slope)

M. disticha

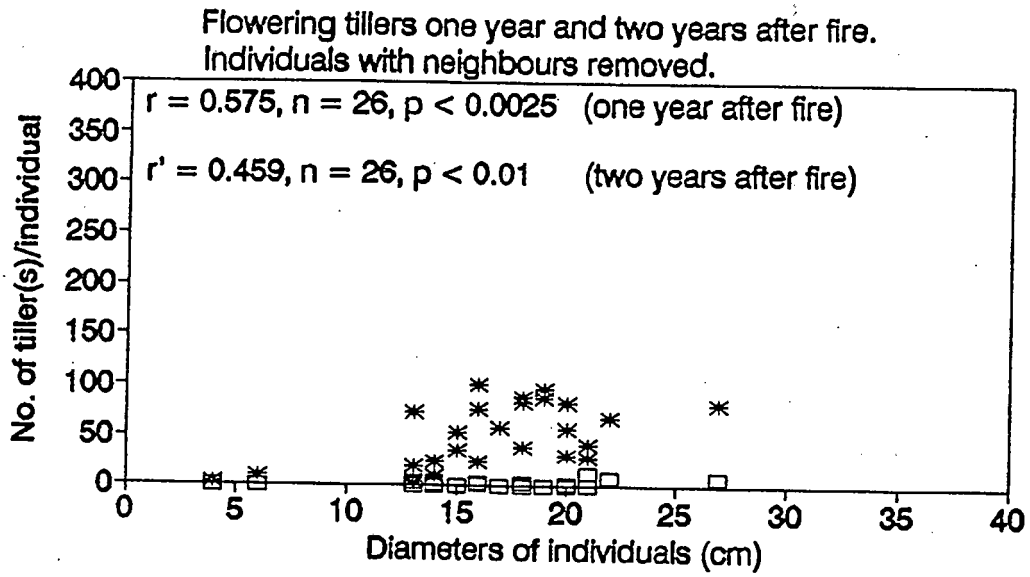


Fig.8.2: Size-number of flowering tillers regression for grass species named above.

* Tillers 1yr after. □ Tillers 2yrs after.

8.5: DISCUSSION

Flowering was more abundant in a one year burn than in a two year burn for all species. An increase in flowering frequency following fire has been noted on the Florida Lake Wales Ridge for a number of grass species (*Aristida stricta*, *Panicum abscissum* and *Andropogon* spp.). Late spring and summer fire stimulated a vigorous flowering response, whereas winter fires encouraged only a vegetative response (Abrahamson 1984). Frequent burning has been reported to stimulate flowering (Daubenmire 1969; Rowley 1970; Vogl 1973; Dickingson and Dodd 1976; Christensen 1981; Gill 1981b; Gunderson et al 1983; Whelan 1986). Within species, both timing of flowering (Curtis and Partch 1950; Gill and Ingwerson 1976; Abrahamson 1984), and number of flowering stems produced (Burton 1944; Stone 1951; Kucera and Ehrenreich 1962) change following fire. Though there are reports of a number of studies on flowering phenologies in fire-dominated habitats (Parrish and Bazzaz 1979; Anderson and Schelfhout 1980; Tepedino and Stanton 1980; Rabinowitz *et al.* 1981) the significance of fire upon flowering of coexisting species is still not yet fully established.

The fact that all the three grass species on the 1988 burn produced out-of-season flowering tillers, regardless of whether neighboured or non-neighboured, suggests a possible post-fire improvement in soil nutrients (Christensen and Muller 1975).

Growth improvement and out-of-season leaf greening observed on a one year burn, compared to two and 15 years after fire, signifies the importance of fire on these aspects. Many C_3 and C_4 plants have been reported to show both an out-of-season growth and leaf greening as a consequence of fire (Pierce and Cowling 1984). Some studies (White 1983; Bowman *et al.* 1988) have shown that grass cover is dependent upon frequent burning. Seasonal variation of fire effects (Gill 1981a; Henderson *et al.* 1983; Lovel *et al.* 1983; Snyder 1986, in Platt *et al.* 1988) have been reported. Foliage increase on burned plots and retrogression on unburned plots was witnessed. The current study has demonstrated the role of fire as "space creator", and

as a stimulant of plants' production and reproduction on Signal Hill.

Elimination of T. triandra from pasture has been linked to the absence of fire, and repeated defoliations (Downing 1974); thus suggesting periodic burning for maintaining T. triandra vigour. On Signal Hill, unburned tussocks of T. triandra have become moribund. Downing (1974) found a similar phenomena, and suggested such tussocks would die eventually if fire could be withheld for long enough. Moribund T. triandra tussocks on Signal Hill will eventually die out if no effective management (e.g. periodic burning) could be exercised. Other grass communities of Signal Hill and elsewhere might be similarly affected.

H. hirta on unaltered plots on a 1975 burn continued to grow and flower, whilst their M. disticha and T. triandra counterparts did not. This might be linked to H. hirta having shown highest xylem water potentials relative to the other two species. However, xylem water potentials in this instance were measured once on each of the two plots. Neither sizes nor distances of neighbours of the measured individual species were considered. The number of neighbouring plants per pressure bombed individual, were also not recorded. This might have affected the xylem water potentials of the monitored plants.

The fact that the two C_4 grass species still flowered in a 1975 burn, whilst their M. disticha counterparts did not, appears to suggest a "generalist" strategy by them (C_4) of coping with both warm and cool temperature.

Whether February was the appropriate time for burning the three grass species is in doubt because numerous herbs and shrubs proliferated, and a year after fire most of the spaces formerly occupied by grasses were dominated by herbs and shrubs. In this case (Western Cape) the suitable time for burning could be winter because it is rainy and hence wet, thus fire would not easily exceed predetermined boundaries. Seeds and resprouters will have enough moisture for germination and establishment. Flowering could also be encouraged under

sufficient soil moisture content. However, it could not be verified which season is best for veld burning.

In conclusion, fire was found to enhance growth, production and reproduction of both C_3 and C_4 plants. The C_3 species differ, however, in being completely dependent on fire for flowering and seed production. In other words, C_3 species does not flower at all in old unburnt veld whereas C_4 species do. It therefore would be interesting to determine whether C_4 species successfully produce seed in older veld and whether this seed is capable of establishment.

The importance of low versus high fire intensity was not investigated in this study.

CHAPTER 9

GENERAL CONCLUSIONS

The analysis of pattern and the competition experiments produced similar results in terms of competition hierarchies. There was general agreement amongst all the tests used to study competition, i.e. removal experiments, effect of xylem water potential on carbon uptake, seedling establishment experiments and fire effect on flowering.

Some interspecific distances were found to be greater than intraspecific distances. This supported the observed distribution pattern of populations/communities on Signal Hill, i.e. commonness of monocultures as opposed to mixed stands. This was also reinforced by other experiments, for instance, in the seedling addition experiments, seedlings were found to be growing better closer to conspecific adults than to contraspecific ones. However, there were some differences in the intensity of suppression experienced by seedlings from one stand to the other. These could be explained in terms of sizes of adults that neighboured the seedlings. The bigger the adult neighbour the more intense is the suppression imposed upon an individual neighboured seedling. The preference of seedlings next to their conspecific adults suggests that interspecific competition is stronger than intraspecific competition.

The three types of distributions: regular, aggregated and random were evaluated through the use of a traditional Clark and Evans (1954) method, i.e. calculating a dispersion index (R), or through the use of Simberloff's (1979) modified version of Clark and Evans' (1954) distance-to-nearest-neighbour technique of pattern analysis.

Pielou's (1960) nearest-neighbour analysis technique was used to test for competition between and within plants, by considering a relationship between both inter- and intra-plant distances and the aboveground canopy diameters. In all cases a positive relationship was found between inter- and intra-plant

distances and canopy diameters. In other words, the existence and importance of competition has been shown by this study.

It was also shown that plants compete for water and space, both inter- and intra-specifically. Competition was readily disclosed when the soil was mildly dehydrated, whilst the importance of space for root expansion was demonstrated when neighbours of monitored plants were cleared. Under mild soil water stress there was a decrease in leaf water potentials of neighboured plants. Monitored individuals on altered plots significantly improved their xylem water potentials, thus suggesting a greater soil volume for root extension and a larger available reservoir of soil water.

The role of higher temperature and irradiation optima for C_4 plants, and vice versa for C_3 plants (not carried out in this study) also suggests the importance of competition among plants of differing photosynthetic pathways.

Both intraspecific positive interaction, and interspecific negative interaction, was verified by this study, but the study could not clearly answer questions such as why inferior competitors still coexist with their competitive dominants. One answer might be that C_4 plants (not expected to dominate in the cooler, winter rainfall region) might be capitalizing on the hot, dry summer seasons of the western Cape region, and hence achieving dominance on some other parts there.

The importance of disturbances like fire was to a certain extent, revealed by this study. They (fire and removals) were found to positively affect production and reproduction of both C_3 and C_4 grasses. For example Themeda triandra occurred in small patches on both the slopes investigated. This was attributed to unmanaged burning of the area. The current burning regime supports herbs and shrubs, and consequently grasses (both C_3 and C_4) would be decimated.

From this study it was concluded that C_3 are superior competitors on the east-facing slope of Signal Hill, whilst T. triandra (C_4) is a stronger competitor on the west-facing slope. The distance between H. hirta versus H. hirta was statistically significantly smaller than that between M.

disticha versus H. hirta on the east-facing slope, thus suggesting that M. disticha is a threat to the long-term existence of H. hirta, especially on the east-facing slope. The distance between T. triandra versus M. disticha was larger than that between M. disticha versus itself on the west-facing slope, thus suggesting that T. triandra might outgrow M. disticha on the west-facing slope.

Competition is not the sole factor responsible for the observed grass distribution patterns on Signal Hill because M. disticha still coexists with the other species there. Past disturbance (see Chapter 3) might be contributing to the observed grass distribution patterns.

Generally it was observed that both C_3 and C_4 grasses, herbs and shrubs are advantaged by burning. So a careful study on fire ecology of the different plants is imperative if a better understanding of the ecology of plant species is to be attained. Fire ecology study is necessary because the role of periodic or planned veld burning is thought to preserve pasture grass communities (Scott 1970). Also the indispensability of grasslands and other palatable plants (e.g. grasses such as T. triandra and H. hirta) in stock farming is commonly known.

The monitoring part of this study was short-term (18 months) and many interesting questions remain unanswered. Amongst others are the following:

(i) How often does competition occur?
(ii) At which stage(s) of the life cycle are plant populations/communities affected by competition?
(iii) How valid is the role of competition in structuring species composition on the Hill?

A role of both biotic and abiotic factors in patterning grassland communities has been corroborated by this study. Both competition interaction and disturbance history of Signal Hill is necessary to properly understand the grass population/community patterns on Signal Hill.

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